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CHARACTERS COMMON TO HIGHER PRIMATES AND CHARACTERS SPECIFIC FOR MAN

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INTRODUCTION

THE scientific investigation of anthropoid apes had its inception at the close of the seventeenth century, when Tyson (1699) published his anatomical description of the chimpanzee. All the early students of the "man-like apes" were greatly impressed with the similarity to man of the great apes. Their writings and, particularly, their illustrations emphasize and frequently exaggerate the *human* qualities of the *apes*. Beginning with Darwin, Huxley and Haeckel this emphasis became reversed so that most modern comparative investigations concern themselves with the *ape-like* qualities of *man*. This last and extremely productive period of research on higher primates has somewhat neglected the at least occasionally needed emphasis on the *specifically human* characters of *man*.

The enormous mass of recent work on the degrees of resemblance between different types of primates has brought about a very encouraging and almost universal unanimity of opinion in regard to the problem of the particular group of primates to which man must be assigned. When critically weighed, all pertinent facts at our disposal force us to the conclusion that man's taxonomic place is in the second suborder of primates (*Anthropoidea* or *Simiae*) and here in the second series, the *Catarrhinae*. Again there is no room for doubting that man shows much less resemblance to the first catarrhine family (*Cercopithecidae* or *Lasiopygidae*) than to the remaining families, the *Hylobatidae* and the *Pongidae* which, together with man, constitute the so-called higher primates. It is in regard to the more detailed and most ambitious problem of man's exact relationship to the other higher primates that the many students of this subject have as yet not reached a general agreement. Keith (1934) has recently shown that man's family tree can to-day be constructed with mostly unhesitating and little disputed

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lines up to the common ancestor of all higher primates, but the places of branching of the terminal twigs leading to recent man and anthropoid apes have been subject to widely differing interpretations. A somewhat extreme view has been taken by Osborn (1927) who states: ". . . the better we understand the human anatomy and mechanism of both the hand and foot and the more we learn of the fossil ancestors of man, the less close appears our relationship to the great anthropoid apes. . . ." A figure entitled "Osborn's present theory of the ascent and phylogeny of man" published by Osborn in 1930 shows the ancestral stem of the family tree of higher primates dividing at one and the same level (Oligocene) into the human branch on one side, the gibbon branch on the opposite side, and a common branch for all great apes in the middle. Sharply contrasting with this view is the interpretation of Smith (1924), as represented by a family tree in which the gibbon branch is the first to separate from the line leading ultimately to man, the former being followed by a branch for the orang-utan, then by one for the chimpanzee and, last of all, by one for the gorilla, which diverges from the human branch in the second half of the Miocene period. This claim of the closest kinship of man with the gorilla is also expressed in the following statement by the same author: "Any one who is familiar with the anatomy of Man and the Apes must admit that no hypothesis other than that of close kinship affords a reasonable or credible explanation of the extraordinarily exact identity of structure that obtains in most parts of the bodies of Man and Gorilla." Practically the same pedigree as that by Smith has been adopted by Broom (1930). Based upon his comprehensive survey of anatomical similarities between man and other primates Schwalbe (1923) has expressed the conclusion that man and chimpanzee are not only most alike but were the last to separate phylogenetically and this perhaps not before the beginning of the Pliocene period. The most extreme view in this direction has been reached by Weinert (1932) whose primate family tree shows the chimpanzee as the last anthropoid ape to branch off the line leading to man and this not until the *end* of the Pliocene! These and some of the intermediary interpretations of the phylogenetic relationships between the recent higher primates are shown in Figure 1. Many additional, more or less differing pedigrees have been published, of which only two of the more recent ones may here be mentioned: Based upon his studies on fossil material, Abel (1934) concludes that there exists a sharp demarcation between the phylogenetic lines for chimpanzee, gorilla and man on one side and those for the remaining higher primates, the orang-utan and gibbons, on the other side. In the family tree, proposed by Abel, the African apes and the *Hominidae* are shown to branch from a common ancestral group, the genus *Dryopithecus*. The line leading to the latter separates from the line leading ultimately to orang-utan in the middle Oligocene, and the *Hylobatidae* diverge from the stem of all higher primates in the Eocene period. In striking contrast to this view stand the conclusions by Werth (1921–1928) which are also largely based upon palaeontological evidence. According to this author a common ancestral primate of the Oligocene gave rise to the three great apes on one side and to the early progenitor of the gibbons and man on the other side. Several authors, notably Pilgrim (1915), had previously favored the view that the gibbons stand particularly near the line of human ascent. With the exception of the last example, all these pedigrees by different authors are alike in

regard to the general grouping of the recent higher primates. If man is placed on the extreme left, the two recent African apes are the nearest to man on the right (the gorilla nearer than the chimpanzee according to Smith, 1924, Sonntag, 1924, Morton, 1927, Osborn, 1930, Schultz, 1930a, Broom, 1930, Keith, 1931, and Clark, 1934; and the chimpanzee nearer than the gorilla according to Schwalbe, 1923, Gregory, 1927, Weinert, 1932, Mollison, 1933, and Abel, 1934). The African apes are invariably followed by the orang-utan and the gibbons are found without exception on the extreme right of the pedigrees. This quite generally agreed upon arrangement of the terminal twigs of the family tree is based on the approximate, average degrees of resemblance between the different forms of higher primates. Where some of these recent twigs arise from the older branches and how the latter grow from the common original stem, are the problems in regard to which there still exist marked differences of opinion. Direct fossil evidence, though of invaluable assistance, is unfortunately as yet far too fragmentary to solve these detailed questions in a decisive manner. The at first so promising serum-precipitin tests of the blood have recently been found to be of very limited value in tracing phylogenetic relationships (Zuckerman and Sudermann, 1935, and others).

By comparing the pedigrees in Figure 1 it is seen that the most striking discrepancy among them consists in differences in the relative position of the exact place of separation of an independent phylogenetic line for man. The places of divergence in the evolutionary courses of the other higher primates differ in the various pedigrees chiefly in regard to geological periods, whereas comparatively little in regard to the order of their occurrence. The most essential problem, therefore, is considerably narrowed, namely to the question whether a separate phylogenetic branch for man started before, at the same time as, or after the

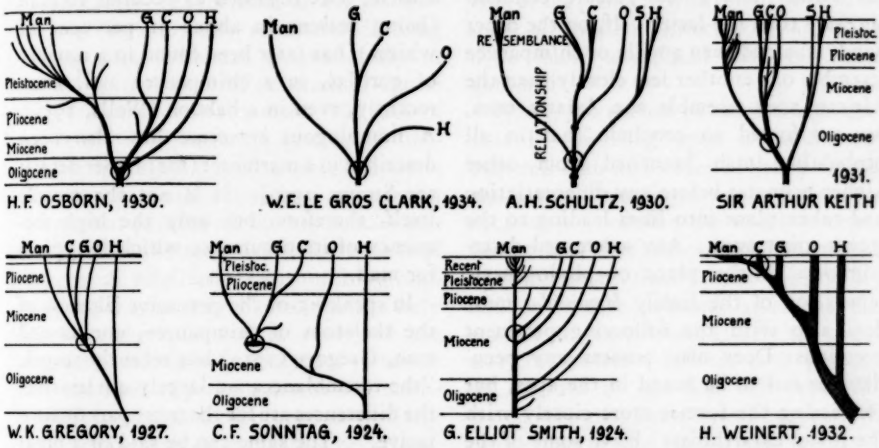

FIG. 1. THE FAMILY TREE OF THE HIGHER PRIMATES ACCORDING TO DIFFERENT AUTHORS

The circles have been added to indicate the place of the last common ancestor of man and any other primate. To facilitate comparisons some of the pedigrees were reversed so that Man appears in all figures on the left side. *G* = Gorilla; *C* = Chimpanzee; *O* = Orang-utan; *S* = Siamang; *H* = Gibbon (or *Hylobatidae* in general).

branches for the recent great apes began to diverge. The answer to this question must rest largely upon a comprehensive and unbiased survey of the *relative* degrees of resemblance between all the different higher primates. If the aggregate resemblance between man and any other recent higher primate is closer than that between any two of the apes, it must be assumed that the former two are taxonomically and genetically more closely related than the latter two and that hence the former had a less remote common ancestry than the latter. If, on the other hand, man and even gorilla or chimpanzee resemble one another less closely than the African apes resemble the Asiatic ones, we are forced to conclude that in all probability man branched from other higher primates before any differentiation had taken place into lines leading to the recent great apes. Any attempted determination of the place of phylogenetic separation of the family *Hominidae* must deal also with the following pertinent questions: Does man possess any peculiarities not to be found in the apes, but connecting the former more closely with the lower catarrhines? Have some of the many evolutionary trends, common to all higher primates, progressed to a lesser degree in man than in the anthropoid apes?

By merely comparing the degrees of resemblance between the various higher primates it is frequently impossible to decide whether some peculiarity of a particular primate represents the retention of a primitive, original condition or a high specialization due to unusually rapid evolutionary change. It is necessary, therefore, to compare the characters studied with the same characters in lower primates. From comparisons between the degrees of similarity of different primates in regard to features which vary individually to a considerable extent no conclusions can be drawn until large series of specimens have been investigated, which supply the chances for finding those sporadic variations which are frequently of decisive significance in the reconstruction of the ancestral genetic endowment of an animal. The discovery of rare individual variations can at times also change the phylogenetic interpretation of features supposedly restricted to only one type of primate. For instance, the *peroneus tertius* muscle, once regarded as peculiar to man (being present in about 91 per cent of whites), has later been found in a number of gorillas, in a chimpanzee and, most recently, even in a baboon (Wells, 1935). A homologous structure has also been described in a marmoset (for further details see Straus, 1930). It is not the muscle itself, therefore, but only the high frequency of its occurrence which is typical for man.

In speaking of the pervasive likeness of the skeletons of chimpanzee, gorilla and man, Gregory (1934) has recently stated: "the resemblances are largely qualitative, the differences are for the most part quantitative." The same can be said of a great many other bodily structures, indeed, one may even claim that the large majority of the characters common to all higher primates are in a restricted sense of a qualitative nature, whereas the characters specific for man or for any other higher primate are in most instances quantitative. Since the quantitative differences between the various higher primates have so far been much less intensively studied than the qualitative similarities and since the former are specially suited for establishing the much needed *relative* degrees of resemblance, this paper will deal predominantly with quantitative characters. Quantitative and, especially, metric methods of investigation are of great help in

taxonomic and phylogenetic problems by, first of all, replacing general impressions, recorded in words alone, by precise measurements, expressed in impersonal figures which can readily be compared with one another. Furthermore, these methods, when skillfully applied, enable the observer to find significant quantitative differences where hitherto we have frequently been content to speak of qualitative likenesses only. For instance, ischial callosities or frontal sinuses are not merely "qualitative" characters of certain primates, but are really structures differing among some primates quantitatively in regard to frequency of occurrence, age of appearance and relative size. The lack of an outer tail represents a qualitative likeness of all higher primates which supports the assumption that they form one natural group, but permits no further conclusions in regard to the more detailed problems of the genetic subdivisions within this group. Help for the latter problems is gained only through the quantitative study of the degrees of reduction in coccygeal vertebrae and muscles. By the quantitative methods of physical anthropology, particularly by investigations of the body proportions, it is possible to demonstrate that all higher primates are qualitatively alike in sharing the same evolutionary trends, such as widening of the shoulders, hips and chest and lengthening of the arms and of the neck, and that they are quantitatively different by having been carried to widely differing levels along the same trends (Schultz, 1933b). It seems quite evident that detailed, quantitative differences can and must change phylogenetically before the more general, qualitative similarities become noticeably altered. In other words, quantitative characters, such as relative size or frequency of a structure, can in most instances change more easily and rapidly during evolution than the apparently more tenacious qualitative features, such as categoric presence or absence of a structure. Many basic qualitative changes are merely the result of preceding and gradual quantitative changes.

The following notes, based largely upon the author's own studies, naturally can not claim to give a final answer to this fascinating question of man's genetic relationship to his nearest simian kin, but are intended merely as a contribution toward the eventual and systematic solution of the problem which will have to rest upon all available information as well as upon many additional data yet to be gathered.

Finally, it should be emphasized again that by dwelling upon the differences between man and other higher primates, the author does in no way contradict or even wish to weaken the widely accepted conclusions that man and the anthropoid apes are more closely related than man and any other primates and that man *resembles* in general most closely the gorilla and chimpanzee. Indeed, it is precisely on account of his firm and repeatedly stated (Schultz, 1927, 1930a, 1931, 1933b) conviction of the unassailable finality of these broad conclusions that the author considers it timely and necessary to turn to the logically following and more detailed problems of man's specific characters and their phylogenetic implications for the determination of man's exact place on the family tree of the comparatively few higher primates.

SIMILARITIES AND DISSIMILARITIES BETWEEN MAN AND ANTHROPOID APES

Human Infants

One of the most persistently quoted and also one of the least justifiable examples of anthropoid ape heritage in man goes back to the well known picture by Robinson, published by Romanes (1892), of a human

infant hanging by its arms and thus "supporting its own weight for over two minutes" and the accompanying statement that this surprisingly great grasping power of the human newborn "refers us to our quadrumanous ancestry — the young of anthropoid apes being endowed with similar powers of grasping, in order to hold on to the hair of the mother. . . ." This temporary grasping reflex in man can not be regarded as indicative of a special anthropoid ape phase in human evolution because, as shown by Richter (1931), the same reflex is much more strongly developed in infantile macaques, which (though no "brachiators") can hang with one hand alone for over thirty minutes. At the age of 2½ months the healthy chimpanzee "Peter" of the Yale Laboratories of Primate Biology could hang by both hands for only one minute (according to the author's examination made with the kind permission of Prof. R. M. Yerkes). This grasping power is of much greater ontogenetic than phylogenetic interest.

There exists, however, another feature, connected with the hands of human infants, which does seem to be of some help in phylogenetic conclusions since it differs radically in different groups of primates. Hrdlička (1928, 1931) has shown abundantly that many human infants walk or run spontaneously on all fours and this invariably with the palms flat on the ground and the fingers completely extended. As shown by Figure 2, this horizontal position of the hands in man is identical with the position of the hands in macaques walking on the ground, but differs very significantly from the upright position of the hands with flexed terminal and middle phalanges in the chimpanzee on all fours. As is well known, the gorilla and the orang-utan also support their weight in quadrupedal position on the knuckles of the flexed fingers and not, as all arboreal lower

FIG. 2. SIDE VIEWS OF ADULT MACAQUE, HUMAN INFANT (after Hrdlička, 1928, Fig. 9), AND ADULT CHIMPANZEE IN QUADRUPEDAL POSTURE, SHOWING POSITION OF HANDS IN WALKING

catarrhines and infantile man, on the wrists with extremely extended phalangeal

and metacarpal portions of the hands. Weidenreich (1931) has already pointed out that in the largely terrestrial baboons and red guenons the body weight is usually supported on the metacarpo-phalangeal joints II to V with the metacarpus held perpendicularly, but with the fingers hyperextended and directed forward, as in all other monkeys, and not backward, as in the great apes. In walking infantile monkeys and apes the hands are already held like in the adults, as is shown, for instance, in the excellent photographs of a baby macaque by Foley (1934), of an infant chimpanzee by Jacobsen, Jacobsen and Yoshioka (1932), and of an infantile gorilla by Reichenow (1921). A photograph of "a baby gibbon learning to walk" (kindly supplied by Miss B. White) shows the animal walking in quadrupedal fashion (a mode of locomotion not practiced by adult gibbons) with the palm on the ground, the hand *extended*, and the fingers *completely straight*.

That the great apes do not place their hands on the ground in the manner of man, gibbons, and macaques is not a mere habit, but an anatomical necessity. This had already been carefully stated by Wilder (1862) who, in dissecting a chimpanzee, had found that: "The tendons of the deep common flexor of the fingers were so short as not to permit the simultaneous extension of both hand and fingers; . . . It also readily accounts for the Anthropoids not being able to apply their palms to the ground when on all fours, but being obliged to rest on the knuckles." On the fresh bodies of macaques and of human beings the hands with completely straightened fingers can easily be extended until they form nearly or fully a right angle with the forearm. On the fresh body of a chimpanzee, however, the fingers become automatically flexed, and this with great force, when one attempts to extend the metacarpal portion of the hand even to only a very slight degree. In a very careful study Virchow (1929) has shown that in the orang-utan the hand (with strongly flexed fingers) can still be extended to as much as 90°, but that in the chimpanzee not even the metacarpal part of the hand can be extended appreciably. Such extension, without releasing the flexure in the fingers, does not become possible until the *palmaris longus*, *flexor carpi radialis* and *flexor carpi ulnaris* have been cut, and even then marked extension is still prevented by a volar ligament between *lunatum* and *capitatum*, a ligament which does not exist in man according to Virchow.

In regard to the attitude of the hands, particularly the fingers, in quadrupedal locomotion and in regard to the anatomical ability to extend the fingers together with the hand man differs radically from the great apes and resembles the gibbons and lower catarrhines.

Ischial Callosities

Even in very recent books on primates (e.g., Weber, 1928; Maurer, 1928; Jones, 1929; Clark, 1934) it is still claimed that ischial callosities occur among the higher primates only in the *Hylobatidae* and that their complete absence in the great apes and man constitutes a primitive condition since "there is no evidence that they have ever passed through an evolutionary stage in which callosities were developed" (Clark, 1934). In 1927 the writer had already collected some of the scattered data by other authors, which show that ischial callosities do exist sporadically among the great apes and he had demonstrated then, and by means of additional material in 1933 (a), that these callosities develop relatively much later in ontogeny in gibbons and siamangs than in the lower catarrhines. In the following notes the

old and new evidence for the occurrence of ischial callosities in the great apes will be briefly reviewed in order to show that we can actually witness the gradual evolutionary disappearance of these structures among the higher primates and that the lack of callosities is not a primitive, but rather a newly acquired condition, which has progressed most among all catarrhines in man.

Friedenthal (1908) was the first author to report the occurrence of ischial callosities in chimpanzees. Lönnberg (1917), in describing a series of ten chimpanzees from the easternmost part of the Belgian Congo, states: "All the adult specimens are provided with very well developed ischiadic callosities." Lorenz von Liburnau (1917) mentions that an adult male chimpanzee from Central Africa (*Pan steindachneri*) possesses ischial callosities 7 cm. in diameter. The occurrence of ischial callosities in the so-called "Tschego" variety of chimpanzee has been reported by Sokolowsky (quoted by Schwalbe, 1923). Bolk (1926) found in a chimpanzee fetus, close to term, two entirely hairless, symmetrical zones over the ischial tuberosities, which he regards correctly as incipient callosities. The writer has observed the same hairless zones in one out of eight chimpanzee fetuses of closely corresponding ages. In a total of 94 chimpanzees (78 embalmed or fresh and 4 living specimens and 12 complete skins; ranging in age from birth to maturity), carefully examined by the author, horny ischial callosities were found in 36 specimens, or in 38 per cent of the cases. One such case is shown in Figure 3. These unquestionable callosities occur in both sexes, at all postnatal ages, and in wild as well as captive specimens; when present they can vary considerably in size and in regard to the thickness of actual horn formation. Among 21 gorillas (14 embalmed, 5 living, and 2 complete skins) of varying ages the author has never seen any trace of these callosities, but Lönnberg (1917) mentions "ischiadic callosities in being" in *Gorilla beringei mikenensis*, consisting of thickened, bare zones on which "the horny layer has a tendency of peeling off in flakes." Among 61 orang-utans (22 embalmed specimens and 39 complete skins) of widely differing ages the author could discover callosities in only 3 cases (= 5 per cent); namely in one infant and in two

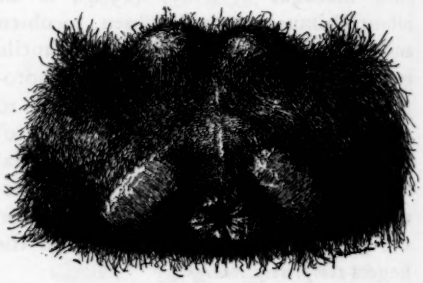

FIG. 3. PERINEAL REGION OF A JUVENILE CHIMPANZEE (Hopkins Coll. No. 387) SHOWING WELL DEVELOPED ISCHIAL CALLOSITIES (Drawn by Mr. J. B. Wilson)

adults in which there existed clearly circumscribed, entirely hairless, and slightly thickened (but not really horny) areas overlying both ischial tuberosities. Friedenthal (1908) has pictured ischial callosities in an adult male orang-utan, but, judging by their corrugated surface, they can not have been really horny.

There can be no doubt that these structures, characteristic of all lower catarrhines and of all *Hylobatidae* (though in the latter they are in general comparatively small and appear late) persist in an atavistic manner in a great many chimpanzees and in an occasional gorilla and orang-utan, though in the last they are but faintly developed when present. In man alone have callosities never been

discovered and never will be since the ischial tuberosities have become completely padded by muscles arising from their entire surfaces, a condition restricted to man and preventing the skin from being pressed directly against bone. It is interesting to find that in regard to the frequency and development of ischial callosities man and chimpanzee stand much farther apart than man and orang-utan.

This conclusion is very similar to that derived from another observation on the perineal region, namely the periodic changes in the so-called sexual skin of females, which are very profound in chimpanzees and many lower catarrhines, whereas completely lacking in man, orang-utan and gibbon (Zuckerman, 1933). Quite recently it has become known that the female sexual skin of the gorilla also undergoes periodic changes, comparable to these changes in the chimpanzee (Raven, 1936, for mountain gorilla and Noback, 1936, for lowland gorilla). It should also be recalled in this connection that in regard to the *labia majora* and the urethro-vaginal tract Wislocki (1932) found a much greater resemblance between man and gibbon than between man and chimpanzee. Finally, it may here be mentioned that man and orang-utan are the only higher primates which can produce excessively long hair. In an adult male orang-utan the author found hair on various parts of the body exceeding 55 cm. in length, a dimension equalled only by the scalp hair of some human beings.

Duration and Rate of Growth

Man and the great apes have in common a striking tendency to prolong the period of growth. As shown by the data in Table 1, the duration of the prenatal portion of growth is in chimpanzee, orang-utan and man from 41 to 66 per cent greater than in the representative of lower catarrhines, the macaque. The postnatal periods of growth have become even more lengthened in the highest primates when contrasted with the lower ones. This increase in the duration of the total period of growth is most pronounced in man and is possibly somewhat greater in the orang-utan than in the chimpanzee.

Based upon the data in Table 1 it can be calculated that of the entire period of growth, from conception to completed eruption of the permanent dentition, 6.2 per cent represent intrauterine life in the macaque, 5.6 per cent in the chimpanzee, and only 3.5 per cent in man. In other words, in relation to the total duration of growth man is born much more early than the chimpanzee or the macaque. In another study the author (1936) has demonstrated that at birth man is very much less advanced in his ossification than the macaque.

The figures in Table 2 show definitely that the relative increases in body weight are not closely correlated to the durations of growth. For instance, the human newborn is on an average more than twice as heavy as a newborn orang-utan, yet the duration of pregnancy is in man practically the same as in the orang-utan. The rate of prenatal increase in size is much greater in man than in the other higher primates. The rate of postnatal growth, on the other hand, is smaller in man than in the chimpanzee and, in all likelihood, the gorilla and the orang-utan. For these reasons the weight of the adult is many more times greater than that of the newborn in the large apes than in man. As shown in the last column of Table 2, the proportion between the body weight at birth and at maturity is very similar in man and the lower catarrhines,

whereas very dissimilar in man and the great apes.

These random notes, discussed so far, have already furnished some striking examples for the contention that man tween man and orang-utan, or between man and gibbon, than between man and chimpanzee. It seems now desirable to consider specifically some of the conditions which have been selected by Weinert

TABLE 1

Tentative data for the durations of some periods of growth in different primates

PRIMATE	DURATION OF PREGNANCY (CONCEPTION AGE)		AGE OF ERUPTION OF FIRST DECIDUOUS TEETH		AGE OF ERUPTION OF LAST PERMANENT TEETH	
	Absolute (Days)	Relative (Macaque = 100)	Absolute (Months)	Relative (Macaque = 100)	Absolute (Years)	Relative (Macaque = 100)
Macaque (Rhesus)	166*	100	0.7	100	6.8*****	100
Gibbon	209**	126	0.9	129	unknown	?
Orang-utan	275***	166	4.5	643	unknown	?
Chimpanzee	235****	141	2.8	400	10.9	160
Man	266	160	6.5	929	19.9	293

All corresponding data for the gorilla are still lacking. * = average of 26 viable newborns, after Hartman, 1932; ** = calculated from data by Ogilvie, 1923 (one case); *** = after Aulmann, 1932 (one case); **** = average of eleven records in recent literature, collected by Schultz and Snyder, 1935 (16 days have been deducted from average "menstrual age" to obtain approximate, average "conception age"); ***** = average of most recent data by author (1936). The original data for the dental ages are reported in detail in another paper by the author (1935).

TABLE 2

Comparisons between body weights at birth and at maturity in different primates

PRIMATE	AVERAGE WEIGHT OF NEWBORN		AVERAGE WEIGHT OF ADULT MALE		RELATION BETWEEN WEIGHT OF NEWBORN AND OF ADULT
	Absolute (grams)	Relative (Macaque = 100)	Absolute (grams)	Relative (Macaque = 100)	
Macaque (Rhesus)	435***	100	9,152***	100	1:21
Langur	780**	179	17,000**	186	1:22
Gibbon	360**	83	5,900**	65	1:16
Orang-utan	1,500*	345	72,000**	786	1:48
Chimpanzee	1,600*	368	60,000*	656	1:37
Gorilla	1,800*	414	200,000*	2184	1:111
Man	3,200*	736	75,000*	819	1:23

* = approximate averages, based upon data in the literature and some additional ones by the author (compiled in part by Schultz, 1927, 1930 b and 1933 b); ** = from weights of specimens in Hopkins collection; *** = averages according to Schultz, 1933 e. That the birth weight of gorilla has not been estimated too low is also evident from the notes by Brandes (1930).

possesses characters in regard to which he resembles the great apes less closely than the latter resemble one another. It has also been already indicated that certain features can differ to a lesser extent be- (1932) as support for his claim that man has so many hereditary characters in common with the chimpanzee to warrant the conclusion: ". . . once there existed an anthropoid ape stem, of whose descend-

ants live to this day chimpanzee and man, whereas all other recent anthropoids had already become divided before this last separation and thereby had not any more acquired the chimpanzee—man—features." (literal translation.)

Frontal Sinuses

A large part of the book by Weinert deals with the frontal sinuses which are regarded as being of greatest significance for phylogenetic deductions since they are claimed to be strictly hereditary features and supposedly not needed for any particular function. Weinert states categorically: "Whereas no orang-utan possesses frontal sinuses, there exists no gorilla and no chimpanzee which is without these sinuses. The frontal sinuses are, therefore, really a feature which divides the anthropoid apes very sharply and without any overlapping of the ranges of variation; but not only that. The more primitive members of the anthropoid apes, namely the gibbons and orang-utans, conform to the condition in the lower primates; the other members, gorilla and chimpanzee, show the same formation as man." After having compared the size and shape of these sinuses in man and the African apes Weinert proceeds: "We must draw the conclusion that the best ancestral form of frontal sinuses is still found in the chimpanzee of to-day and that from this form evolved in diverging directions the frontal sinuses of gorilla and of man." (literal translation.)

Weinert's account of these supposedly very definite and, in that case, phylogenetically quite important conditions requires some corrections. In 1908 Cunningham had already reported the occurrence of a small frontal sinus in an adult orang-utan. In his original paper on frontal sinuses Weinert (1926) describes the conditions in orang-utan as follows: "Measured from the lower border of the *Pars orbitaria* of the frontal bone, the cavity reaches on an average for 5 to 10 mm. up into the frontal bone and thus forms, if one wishes, a small frontal sinus. In an old male I measured once more than 2 cm., whereby the cavity had reached nearly to the upper orbital edge." (literal translation.) Finally, Kleinschmidt (1933) has published a detailed account of frontal sinuses in four orang-utan skulls (one of these cases is reproduced in Figure 4). Some of these rare sinuses in orang-utans reach higher up into the frontal bone than these sinuses do in occasional human beings, in whom they may not even approach the glabellar region, but lie in the frontal portion of the medial orbital walls (see e.g. Schaeffer, 1920, Figure 123). In Kleinschmidt's orang-utan No. 5 the portions of the sinuses surrounded by the frontal bone are certainly larger than the corresponding portions of the vestigial sinuses in the chimpanzee, shown in Figure 4. Furthermore, the skull of the adult pygmy chimpanzee (*Pan paniscus*), described by Coolidge (1933), contains only an extremely diminutive frontal (?) sinus, reaching at best very little above the lower edge of only the orbital part of the frontal bone. Finally, in man the frontal sinuses are known to be totally absent in very rare cases among the higher races, but, according to Turner (1901), in 30.4 per cent of Australian aboriginals.

It is quite evident from these notes that a trend for the formation of frontal sinuses is manifest in man and all the great apes, including the orang-utan, but that this tendency is least pronounced in the orang-utan and possibly no more so in pygmy chimpanzees. The differences in regard to frontal sinuses, existing among the great apes and man, are purely quantitative and relate merely to frequency of

occurrence and size and location of structure. It is well known that the size of the sinuses in man can vary between total absence and such enormous figures for cubic contents as easily surpass any maximum values for chimpanzee. The story of the frontal sinuses is in accord with the general assumption of a common origin of hair man resembles the three great apes much less than the latter resemble each other (Schultz, 1931a), or the findings that among all higher primates man alone lacks sinus hairs (Friedenthal, 1908), that curly hair is a human peculiarity, that man is the only primate with *ossicula mentalia* in the mandibular sym-

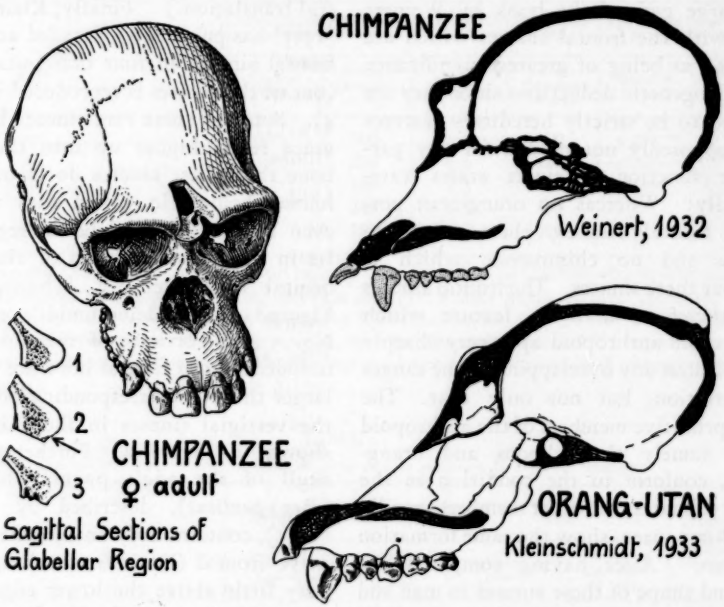

FIG. 4. LEFT: SKULL OF SMALL, BUT ADULT, FEMALE CHIMPANZEE FROM UNKNOWN LOCALITY (Labor. Phys. Anthropol., Hopkins Univ.) WITH BLOCK OF BONE REMOVED FROM GLABELLAR REGION TO SHOW THE DIMINUTIVE FRONTAL SINUS

Sagittal sections: 1 = 3 mm. medially from left end of block; 2 = midsagittal plane (arrow points to *nasion*); 3 = right end of block; 1 and 3 show the upper ends of the left and right sinuses.

RIGHT: MIDSAGITTAL SECTIONS OF SKULLS OF (ABOVE) CHIMPANZEE (PRESUMABLY OLD MALE) AFTER WEINERT (1932, FIG. 20), SHOWING ENORMOUS FRONTAL SINUS, AND (BELOW) OLD MALE ORANG-UTAN AFTER KLEINSCHMIDT (1933, FIG. 5), SHOWING AN UNQUESTIONABLE FRONTAL SINUS

for man and all the great apes, but does not prove Weinert's specific claim that chimpanzee and man were the last higher primates to separate. That man resembles most closely the chimpanzee in regard to merely the *average size and shape* of the sinuses carries no greater weight phylogenetically than, e.g., the fact that in regard to the general density and amount physis of newborns, that only man possesses a transverse metatarsal ligament between toes I and II (Jones, 1929), and that a true inguinal ligament is exclusively a human character (Stewart, 1936).

Wrist Bones

After having given the usual and well-known account of the *os centrale* in pri-

mates, Weinert concludes: ". . . since normally the anlage of an Os centrale is not any longer present in gorilla, chimpanzee and man, this loss can be attributed only to a modification in their original inheritance, a change which took place only *once* and which to this day concerns gorilla, chimpanzee and man. The branch of the orang-utan was not affected by this loss, it must hence have become separated earlier and could not any more participate in the evolution of man." (literal translation.)

this carpal element. Leboucq (1884) mentions two cases of *Hylobates leuciscus* in which there is no free *os centrale*, but merely a nodule on the *naviculare* which may correspond to the *centrale*. In another specimen of this same species (a Java gibbon and not a siamang, as pointed out by the writer, 1933a) Boltze (1926) found the *centrale* to be completely fused with the *naviculare*. In an old siamang, finally, the author discovered complete fusion between the latter two bones on one hand (see Figure 5) and nearly complete fusion

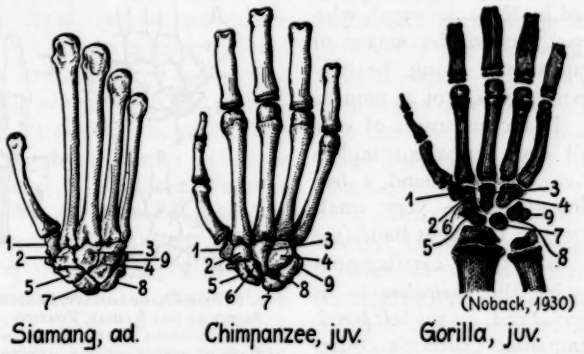

FIG. 5. LEFT: DORSAL VIEW OF WRIST AND METACARPUS OF AN OLD SYMPHALANGUS SYNDACTYLUS (Author's Coll.) WITH COMPLETELY FUSED (OR LACKING?) OS CENTRALE; MIDDLE: HAND SKELETON OF JUVENILE CHIMPANZEE (Hopkins Coll.) WITH OS CENTRALE; RIGHT: HAND SKELETON OF JUVENILE GORILLA WITH OS CENTRALE (after X-ray photograph by Noback, 1930)

1 = *multangulum majus*, 2 = *multangulum minus*, 3 = *capitatum*, 4 = *hamatum*, 5 = *naviculare*, 6 = *centrale*, 7 = *lunatum*, 8 = *triquetrum*, 9 = *pisiforme*.

The following compilation of old and new facts will demonstrate that Weinert's conclusions again require some very significant corrections. Among *Hylobatidae* the *os centrale* has been reported to be totally lacking, or else completely fused, in a considerable number of specimens. Thus, Lucae (1865) has figured a *Hylobates leuciscus* without an *os centrale*. Giebel (1879) states that among higher primates, including the gibbon, the orang-utan alone possesses the *centrale*, so it must be assumed that this careful observer happened to examine a gibbon without

on the other hand. It is, unfortunately, impossible at present to determine adequately the relative frequency of fused (or lacking?) central bones in *Hylobatidae*. Boltze observed this condition in one out of three adult specimens and the writer in one out of six skeletons, specially examined for the carpus, but the latter series contains two juveniles in which fusion is less likely to occur than in fully adult or old animals.

That the *os centrale* can fuse completely with the *naviculare* in the orang-utan, has been shown by Leboucq (1884), who

describes this condition in the ligamentous carpus of an adult. Incidentally, in a detailed study Virchow (1929) has demonstrated that the *os centrale* of orang-utan stands in regard to its topographic relations between the lower catarrhines and man.

As the disappearance of a free *os centrale* in the Asiatic anthropoid apes is most likely to occur in old specimens, so the persistence of this ossicle in the African apes is most apt to be encountered among very young animals. For the gorilla such persistence of a free *centrale* in each hand has been reported by Noback (1930), who found this carpal element by means of X-ray photographs in a living, healthy animal of the estimated age of 42 months (see Figure 5). In a chimpanzee of very similar age (all first permanent molars fully erupted) the author found a free *centrale*, containing only a very small ossification center, on the right hand (see Figure 5) and an entirely cartilaginous *centrale*, fused with the *naviculare* at its proximal and dorsal end, on the left hand. In another chimpanzee (author's collection) of the same dental age there exist on both hands between *multangulum minus*, *capitatum* and *naviculare* cartilaginous nodules which are partly fused with the navicular bones. That these nodules represent the central bones at a stage of belated fusion appears unquestionable, since no corresponding structures were present in five additional infantile and seven juvenile chimpanzees which had been examined by the author before they were macerated. Hartmann (1883) found in a "very young" chimpanzee the articular surface of the *naviculare* to be segmented by two transverse furrows, though the bone contained only one ossification center. In the light of the above facts it seems quite possible that this constitutes nearly completed fusion of the *centrale*. In three chimpanzee fetuses of the Hopkins collection, corresponding in development to human fetuses of the seventh and eighth lunar month, there exists an *os centrale* in every case, as shown by Figure 6. In two of these fetuses the *centrale* is entirely free (in *A* it is very small and was hidden from view until the dorsal part of the *naviculare* had been removed); in the third fetus (*B*) the cartilages for *centrale* and *naviculare* are incompletely separated by a cleft, i.e., fusion has started at the proximal end of the *centrale*. Such clefts,

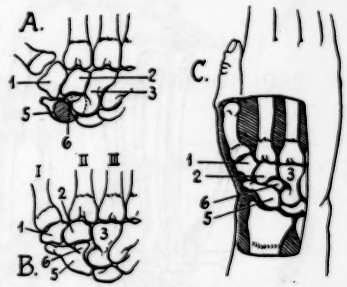

FIG. 6. SEMI-DIAGRAMMATIC SKETCHES OF THE DORSAL ASPECT OF THE RADIAL PORTION OF THE ENTIRELY CARTILAGINOUS WRIST BONES IN CHIMPANZEE FETUSES OF THE HOPKINS COLLECTION

A = No. 302; 214 mm. sitting height. The dorsal half of the *naviculare* (indicated by dotted line) has been cut away (at shaded area of "5") to show the hidden *centrale*. *B* = No. 390; 225 mm. sitting height. *C* = No. 394; 250 mm. sitting height. Numbers for the wrist bones as in Figure 5.

indicating incomplete coalescence between *centrale* and *naviculare*, have been found in a number of adult human skeletons (e.g., Pfitzner, 1895, Figs. 9, 12 and 13; Virchow, 1929, Fig. 24; Forster, 1933/34, Figs. 4, 5 and 6). The frequency of the persistence of entirely free central bones in adult man differs between a mere fraction of one per cent and three per cent according to different authors.

From the investigations of Rosenberg, Leboucq, and others we know that the *os centrale* appears regularly in the human embryo and that, as a rule, it fuses com-

pletely with the *naviculare* during the third month of prenatal life. From the notes assembled above it appears most probable that in chimpanzee (and gorilla?) this fusion between *centrale* and *naviculare* does not begin until late in fetal life. Indeed, it seems possible that the *average* age of completed fusion lies in the infantile period. Very few hand skeletons of chimpanzee and gorilla infants have been thoroughly examined before maceration, i.e., before the frequently cartilaginous and diminutive *centralia* might become lost or dried and shrivelled beyond recognition, yet we already possess two records of free and one of incompletely fused central bones in animals at least three years old. In orang-utan and, particularly, in the *Hylobatidae* the *centrale* can fuse with the *naviculare* during middle or old age. In lower catarrhines the author has never found such fusion, even in skeletons of very old animals, and has never seen a report describing such cases. It appears, therefore, that the various higher primates have in common a tendency to fuse the *centrale* with the *naviculare*, but differ quantitatively in regard to the age at which this tendency manifests itself and in regard to the proportion of individuals affected by this tendency at the differing ages. To the student of growth the difference between the ages of fusion of the *centrale* in man and in chimpanzee (very early and, at least, late intrauterine development) is as significant as the difference between the ages of fusion in chimpanzee and gibbon (late fetal or infantile life and old age).

Many normal growth changes in the skeleton differ very strikingly among the different types of catarrhines in regard to the relative ages at which they occur. For instance, the facial portions of the sutures between the premaxillary and maxillary bones disappear in man very much earlier than in any other catarrhines. In the anthropoid apes the same tendency toward early obliteration of these sutures manifests itself in widely varying degrees, as has been abundantly demonstrated (e.g., Ashley-Montagu, 1935). The suture between the two nasal bones obliterates during fetal life in the macaque, usually during early juvenile life (occasionally not until late juvenile life) in the anthropoid apes, and in old age alone, and then only in very rare cases, in man; the metopic suture closes as a rule at comparatively later ages in man and the macaque than in the great apes; and the great fontanelle becomes closed at a much more advanced stage of growth in man than in any other primate (Schultz, 1936). The story of the *os centrale* is merely another instance of such differences in the ages at which skeletal growth changes take place, but this particular growth change, i.e., the tendency toward fusion between the two carpal elements, is clearly restricted to the higher primates.

There exist innumerable other conditions which reveal evolutionary trends common to all higher primates and at the same time have attained widely differing degrees of perfection in the various types. Obviously, Weinert has selected and overemphasized conditions which happen to have reached more or less similar phylogenetic levels in man and the African apes, and he has grossly neglected many other conditions in regard to which man stands removed from chimpanzee and gorilla.

Coccygeal Vertebrae

Extreme reduction in the number of segments of the caudal portion of the spinal column exists in all the higher primates, but this evolutionary specialization has progressed to different extremes in the various genera. Weinert states

in this connection: "Gorilla and chimpanzee have as a rule five coccygeal vertebrae, man four, and the two Asiatic anthropoids only three. . . . Man can not have descended from gibbon or orang-utan, not have branched from a form which has fewer tail vertebrae than he himself; it is impossible that a rudimentary structure, which has already become reduced in its entirety, is subsequently again enlarged in man; i.e., increased by one vertebra. Gorilla and chimpanzee, however, show in the total composition of their spinal column, including the tail, a picture which is not only possible, but can have been expected, as a step preceding the conditions in man" (literal translation). For those who believe in the absolute irreversibility of evolution this might sound convincing, though it should be remembered that in embryonic life man still possesses 8 or even more caudal segments and that gibbon and orang-utan had ample time to reduce the number of their tail vertebrae *after* their separation from any line leading to man. The chief weakness, however, of Weinert's conclusions consists in the fact that his underlying data do not at all represent the typical conditions. These data are apparently copied from Fischer, who (even in a paper of 1933) states that his figures for the numbers of vertebrae in primates are in general based upon the data by Rosenberg, i.e., upon data which are far too scanty to furnish reliable averages. In 1930 (a) the writer published comprehensive statistics for the numbers of vertebrae in primates, which included the many scattered data from the literature as well as very considerable series of new records. The latter records have recently been combined with many new data by the author's colleague, Dr. W. L. Straus, Jr., who has kindly supplied the writer with the following new averages for the numbers of coccygeal vertebrae in anthropoid apes. These averages are based exclusively upon records of specimens in which there could be no doubt in regard to the exact number of true coccygeal vertebrae.

PRIMATE:	NUMBER OF SPECIMENS:	AVERAGE NUMBER OF COCCYGEAL VERTEBRAE:
Man	745	4.2
Chimpanzee	47	3.2
Gorilla	69	3.0
Orang-utan	56	2.8
Gibbon	47	2.7
Siamang	13	2.6

If Weinert's sanguine reasoning were to be applied consistently to these new averages, one would have to draw the absurd conclusion that all the anthropoid apes originated from man-like ancestors!

It is significant that in regard to the number of coccygeal vertebrae man differs more from all the anthropoid apes than any two of the latter differ from one another.

Relative Cranial Capacity

As further support for his claim of the extremely close relationship between man and chimpanzee, Weinert gives a table of cranial capacities (cu. cm.), body weights (g.) and the proportions between the two. According to his figures the relation between the cubic contents of the brain case and the body weight equals among adults 1:40–60 in man, 1:150–200 in chimpanzee, 1:400–600 in gorilla, 1:300 (?) in orang-utan, and 1:100 in gibbon. Since the gibbon should not be compared on account of its small general size, Weinert points triumphantly to another instance of greatest resemblance between man and chimpanzee. If this particular proportion is to be used at all for phylogenetic deductions, it must be based either upon capacity and weight in the same individuals or else upon averages for

capacity and averages for weight which are derived from very extensive series of observations. The relation between cranial capacity (or the only approximately corresponding brain weight) and body weight varies enormously, chiefly on account of the latter factor. The age changes of this proportion are very profound since, particularly in apes, the brain increases comparatively little after infantile life, whereas the body weight can continue to rise very markedly even after growth in height has ceased. Incidentally, among newborns the orang-utan surpasses man in relative cranial capacity. The ratio between capacity and body weight equals in a newborn orang-utan approximately 1:7.7 and averages in newborn whites 1:8.6. These figures demonstrate also the tremendous postnatal changes in this ratio (adult man = 1:40–60).

In a previous paper the writer (1933a) has given the cranial capacities and body weights of large numbers of *Hylobatidae*. In the subgenus *Hylobates* alone the capacity of 77 adults averages 97.5 cu. cm. and the body weight of 52 adults averages 5900 g., resulting in a proportion of only 1:61 (instead of 1:100, as claimed by Weinert) for true gibbons. In an old male orang-utan (P.A.L. 101) the capacity is 450 cu. cm. and the body weight is 77.1 kg., thus the proportion amounts to only 1:171 and not to 1:300. In one of the two adult male orang-utans, carefully described by Milne-Edwards and others (1895), the capacity is 470 cu. cm. and the body weight is 65.5 kg.; the ratio, therefore, is only 1:139. For adult male chimpanzees an approximate, average ratio may be obtained from their average cranial capacity of 404 cu. cm. (Oppenheim, 1912) and their average body weight of 60 kg. (Table 2). The resulting ratio equals 1:149. In a practically adult (only third molars not yet erupted) female mountain gorilla (P. A. L. 7) the capacity is 462 cu. cm. and the body weight is 72.6 kg.; the proportion between these data equals 1:157.

The ratio between the actual brain weight and the body weight averages quite approximately 1:50 in adult man and amounts to 1:114 in a very small, but adult, female chimpanzee (Fulton and Keller, 1932). It averages 1:112 in ten adult female orang-utans (Connolly, 1932), but equals 1:186 in a male orang-utan, weighing 73.5 kg. (Dubois, 1914). The giant male gorilla "Bobby" of the Zoological Garden in Berlin is reported to have had a body weight of 267 kg. and a fresh brain weight of only 610 g., i.e., a ratio between the two of 1:438. In the above mentioned female mountain gorilla this same ratio can not have been much over 1:175 (assuming that brain weight in g. equals approximately 90 per cent of cranial capacity in cu. cm.).

These figures suffice to show that the relation in size between brain and body does not separate the great apes to the extent, claimed by Weinert, since the enormous ranges of individual variations can overlap in all three types, particularly if both sexes are considered. If the most man-like ratio of the gibbon is excluded from these comparisons and quite properly regarded as partly due to the gibbon's small general size, then the ratio of giant male gorillas should also be omitted on account of its being influenced by extreme body size. There remains, therefore, only one safe and well established conclusion, namely that adult man possesses a relatively larger brain than other adult primates of similar body weights, i.e., orang-utans, chimpanzees and female gorillas. Differences in relative brain size among these great apes most likely exist in the *average* values, but are certainly not

as great as the difference between man and any of the anthropoids of comparable body weight.

Os Penis

A rod-shaped bone of varying size occurs in the penis of all simian primates, except in some platyrrhines and in man. In very rare cases a penis bone can occur in man, but probably only as a pathological, rather than as an atavistic, formation (see e.g. Jacobi, 1899). Weinert (1932) pictures a small penis bone of an adult chimpanzee and a large penis bone of an adult orang-utan and states: ". . . it is again the orang-utan which, with its comparatively large bone, is farthest removed from man, whereas the chimpanzee, with the smallest ossicle, occupies again the nearest step." The following facts regarding the length of the penis bone in chimpanzee and orang-utan are compiled from the literature and from the author's own observations: Length of *os penis* in adult chimpanzee = 8.5 mm. according to Weinert (1932); 9 mm. in a sub-adult specimen (Hopkins coll. No. 392, 3rd molars not yet erupted) weighing 40.2 kg.; 10.5 mm. in an adult specimen (Hopkins coll. No. 206) weighing 43.8 kg. and measuring 48 inches from crown to heel; "a little more than half an inch long," i.e., at least 13 mm., in an adult, measuring 47 inches from crown to heel, dissected by Sonntag (1923). Length of *os penis* in adult orang-utan = 12 mm. according to Weinert; 12 mm. in another specimen, according to Pohl (1928); 15 mm. in a specimen, weighing 73.5 kg., described by de Pousargues (1895); "smaller than in de Pousargues' specimen" in two adults, one of which weighs 76.5 kg., described by Fick (1895); 11 mm. in a specimen (Hopkins coll. No. 212) weighing 77.1 kg. The last penis bone is at least as slender and pointed as those pictured by Pohl and by de Pousargues and is not nearly as thick and blunt as the specimen pictured by Weinert.

It is readily seen that there exists no justification for concluding that the penis bone of the chimpanzee is appreciably smaller in proportion to the size of the animal than that of the orang-utan. We possess records on a chimpanzee with a penis bone at least 13 mm. long and on a fully grown orang-utan in which this bone measures only 11 mm. The latter animal weighs over 77 kg. and in a chimpanzee of only 44 kg. the penis bone is 10.5 mm. long.

These notes on the *os penis* add another instance to the list of characters which differ far more between man and any of the great apes than the latter differ among themselves. The complete lack of a penis bone, as the universal absence of ischial callosities and of sinus hairs, is at least among higher primates a specifically human character which removes man from as close a proximity to the chimpanzee as has been claimed by Weinert and others.

Kidney

In a chapter dealing with the papillae of the kidney Weinert maintains that it is again the chimpanzee in which the conditions of man are foreshadowed. In a comprehensive and careful study of primate kidneys Straus (1934) has reached a quite different conclusion. He states: "He (Weinert) attempted to show that in the structure of the kidney (i.e. number of papillae), among other points, the chimpanzee more closely approaches Man than does any other Primate. A critical examination of the available evidence, however, shows plainly that neither the chimpanzee nor any other anthropoid ape can be regarded as suggesting the human form of kidney. Consideration of Primate kidneys from a phylogenetic aspect

merely emphasises the unique and isolated position of Man. The only approach to the human condition is made by the spider monkey, . . ."

Menstrual cycle

Weinert states that the chimpanzee and man have the same duration of the menstrual cycle, i.e., 28 days. According to all available information (collected by Schultz and Snyder, 1935) and on the basis of the latest records from the Johns Hopkins colony of living chimpanzees the writer is convinced that the *average* menstrual period of these apes amounts to considerably more than 30 days. A brief report by Tomilin (1936), which has just appeared, gives as average for 50 normal menstrual cycles of the chimpanzee 35.5 days. In orang-utan this period averages 32 days (Aulmann, 1932), whereas in the macaque 28 days (Hartman, 1932). It appears, therefore, that in regard to this feature man and macaque are alike, but differ from orang-utan and chimpanzee.

Weinert's work has been selected for this critical review merely because it represents one of the most ambitious and comprehensive attempts to determine man's exact place on the family tree of higher primates. Ample evidence has been discussed above to show that Weinert's widely accepted conclusions rest on many data which are at times insufficient and in part incorrect. The pertinent facts at our disposal justify the conclusion that *in general* man resembles somewhat more closely the African anthropoid apes than any other primate, but they do not justify the more specific conclusion of Weinert that the resemblance between man and chimpanzee is much closer than, or even as close as, the aggregate resemblance between the African apes and the orang-utan. There exists as yet no unimpeachable evidence for the assumption of Schwalbe and of Weinert (most recently also accepted by Gieseler, 1936), that man and chimpanzee have been the last higher primates to become phylogenetically separated and this at a comparatively recent date.

DEGREES OF RESEMBLANCE BETWEEN THE HIGHER AND THE LOWER CATARRHINES AND BETWEEN MAN AND THE ANTHROPOID APES

In an attempt to establish tentatively the degrees of resemblance between the various higher primates in regard to their quantitatively measurable characters it is essential to find a type of lower catarrhine which shows most closely (even though at best only approximately) the original and hence primitive conditions. The macaque can be regarded as the most suitable, generalized representative of the lower catarrhines. This conservative primate has had no share in the many, minor specializations in structure and habit which characterize most of the other forms of the *Cercopithecinae* and all the genera of the *Semnopithecinae*. At least in regard to the proportions of its outer body and those of its skeleton the macaque, particularly the Rhesus monkey, has probably deviated comparatively little from the conditions which we can assume to have existed in the ancestral type of lower catarrhine from which all later higher primates originated.

By expressing the quantitative characters of the higher primates in percentage of the corresponding conditions in the macaque, a method is obtained by which not only the direction of the approximate phylogenetic change becomes evident, but also the comparative degrees of evolutionary change in different characters as well as the relative amounts of

difference between the various higher primates.

Spinal Column

The numbers of vertebrae in the different regions of the spinal column furnish for man is 17.0, or 10 per cent smaller than in the macaque. If the former average is assumed to equal 100, the latter average will appear on the same scale at 90, and the corresponding average for the orang-utan (16.0) at 84.7. Figure 7

TABLE 3

The averages of the numbers of vertebrae in the thoracolumbar and sacral regions of the spine in different primates and the percentage differences between the averages of the Macaque and those of the other primates

PRIMATE	NUMBER OF SPECIMENS	THORACOLUMBAR VERTEBRAE		SACRAL VERTEBRAE	
		Average number of vertebrae	Percentage difference from Macaque	Average number of vertebrae	Percentage difference from Macaque
Macaque	53	18.9	0	3.0	0
Langur	49	19.0	+0.5	2.9	−3.3
Gibbon	81	17.9	−5.3	4.4	+46.7
Siamang	23	17.4	−7.9	4.5	+50.0
Orang-utan	83	16.0	−15.3	5.1	+70.0
Chimpanzee	63	16.8	−11.1	5.4	+80.0
Gorilla (*G. gorilla* + *G. beringei*)	104	16.6	−12.2	5.6	+86.7
Man	3856	17.0	−10.0	5.2	+73.3

The data for the Langur have been kindly supplied by Dr. W. L. Straus, Jr., those for the Macaque, Orang-utan, Chimpanzee, and Man are from the author's paper of 1930 a, those for the Gibbon and Siamang from the author's paper of 1933 a, and those for the Gorilla from the author's paper of 1934.

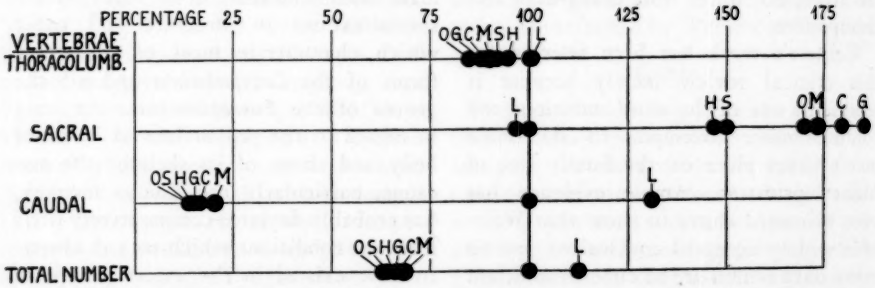

FIG. 7. DIAGRAMMATIC REPRESENTATION OF THE AVERAGE NUMBERS OF VERTEBRAE IN HIGHER PRIMATES IN PERCENTAGE RELATION TO THE CORRESPONDING AVERAGES IN THE MACAQUE

Explanation of the abbreviations in this and all following, similar figures: *L* = Langur, *H* = Gibbon, *S* = Siamang, *O* = Orang-utan, *C* = Chimpanzee, *G* = Gorilla (both species combined; in case the species are shown separately, *G* stands for only *Gorilla gorilla* and *B* for *G. beringei*); *M* = Man. The macaque is always shown on the perpendicular line, representing 100 per cent.

a simple example of this method for demonstrating the quantitative differences between various primates (see Table 3 and Figure 7). The average number of thoracolumbar vertebrae amounts to 18.9 in the macaque; the corresponding average and all the following, similar figures are constructed according to this principle and by means of these simple calculations. Figure 7 shows very clearly that in regard to the numbers of vertebrae all the higher primates have become removed as one

group from the lower catarrhines, though the exact degrees of deviation differ in the various types. The numbers of thoracolumbar and of caudal vertebrae and the total numbers of all vertebrae have become reduced in the higher primates, as compared to the lower catarrhines, whereas the numbers of sacral vertebrae have become increased. The relatively greatest changes have occurred in the sacral and caudal portions of the spine. On the basis of the justifiable working hypothesis that the numbers of the vertebrae in the various regions of the spine are at most very little different in the macaque (or in any other lower catarrhine, since they are all remarkably uniform in this respect) and in the common ancestor of all higher primates, it can be concluded that the phylogenetic change from the original condition has been smaller in man than in any anthropoid ape in regard to the number of the caudal vertebrae and the total number of vertebrae, that the change has been smaller in man than in the great apes in regard to the number of thoracolumbar vertebrae, and that it has been smaller in man than in the African apes alone in regard to the number of sacral vertebrae. Man, therefore, is revealed as comparatively primitive in the numbers of his spinal segments. It is also very significant to find from Figure 7 that the differences between the two representatives of the two subfamilies of the lower catarrhines are always much smaller than the differences between either of the two and any of the higher primates.

Not only the numbers of the vertebrae are of interest in studying the resemblances between different primates, but also the relative lengths of the various regions of the spine. Table 4 contains preliminary data on these relative lengths, which were obtained by the author on fresh or embalmed bodies by measuring with a tape along the ventral side of the intact spinal column between the centers of the intervertebral disks at the ends of each spinal region while the bodies were carefully placed flat on their backs to avoid changes in the curvature of the spine which stretch or compress the intervertebral disks. Even though the figures for the higher primates, besides man, are as yet based upon single specimens only, it can be stated that, in proportion to the anterior trunk height, the cervical region of the spine has become greatly lengthened in man and all three great apes in contrast to the macaque (and some other lower catarrhines, not listed in the table), the

TABLE 4

*Preliminary data showing the relative lengths of the various regions of the spinal column**

ADULT PRIMATE	LENGTH OF SPINAL REGION IN PERCENTAGE OF TRUNK HEIGHT					
	Cervical	Thoracic	Lumbar	Thoracolumbar	Sacral	Caudal
Macaque (Average of 5 *Pithecus rhesus*)	17.6	42.4	45.1	87.5	11.4	69.3
Gibbon, ♂	16.9	40.2	24.6	64.8	13.7	4.6
Orang-utan, ♂	24.1	49.8	23.9	73.7	27.9	6.2
Chimpanzee, ♂	23.5	51.1	17.2	68.3	29.4	8.6
Gorilla (*beringei*) ♀	23.7	49.8	27.7	77.5	26.4	9.2
Man (Average of 9 Negroes, 1 White, 1 Filipino)	25.9	53.9	37.3	91.2	25.8	6.3

*(Measured with tape between centers of intervertebral disks at ends of spinal regions) in different adult primates (all fresh bodies, except gibbon and orang-utan which had been embalmed).

thoracic region of all higher primates has become somewhat increased in length, whereas the lumbar region has become shortened to a slight extent in man and to a tremendous extent in the gibbon and the large apes. As is to be expected from the increase in the number of vertebrae participating in the formation of the sacrum of the higher primates, the relative length of the sacral region is much greater in man and the apes than in the macaque. In regard to the relative length of the thoracolumbar portion of the spine man and macaque are practically alike and stand in sharp contrast to the much lower figures for the gibbon and the great apes. In this respect, therefore, man differs much more from any of the great apes than the latter differ among themselves.

Proportions of the Trunk and Neck

By the same considerations and methods, as outlined above, the more significant body proportions have been calculated as percentage differences in relation to the conditions in the macaque. The absolute values of these proportions and their changes during postnatal growth have already been published by the author (1933 b) or will be recorded in future papers. The interest here is centered upon the relative differences between the proportions of different primates at birth and at the completion of growth. It may be merely mentioned that the relative differences between adults are based upon averages derived from measurements on two to nine specimens for each type of primate, whereas those between newborns are based only upon the data for single specimens, with the exception of man, who is represented by the averages of ten white and ten negro newborns. The methods, by which the measurements and their proportions have been obtained, are fully described in a special paper by the author (1929). The anterior trunk height (from suprasternal notch to upper end of pubic symphysis) is most frequently employed in proportions which intend to free other measurements from the factor of general body size, because it is by far the most suitable and accurate dimension that can be chosen for comparative studies on primates.

The first proportion in Figure 8, the relative chest circumference, amounts in the newborn macaque to 138.8 and in the newborns of higher primates to anywhere between 168.6 and 208.4. The latter values equal from 121.5 to 150.2 per cent of the value in the macaque and appear as these percentages in Figure 8. In the adult macaques the relative chest circumference has decreased on an average to 103.0 and the averages of the adult higher primates fluctuate between 148.8 and 223.4, i.e., between 144.5 and 216.8 per cent of the average in adult macaques. These examples suffice to illustrate the precise construction of these diagrams for the relative differences in body proportions.

All the proportions of the trunk and neck, shown in Figure 8, separate the higher primates from the lower catarrhines and demonstrate that the former have departed from the conditions in the latter in one and the same direction, but this to widely differing degrees. In regard to all these proportions the adult higher primates deviate more from adult macaque than the newborns of the former deviate from newborn macaque. Already at birth, however, are the differences between the higher and the lower forms clearly apparent, these differences becoming merely more accentuated during postnatal growth. In comparison with the macaque, or langur, in all higher primates the chest girth is relatively much greater, the shoulders and hips are

proportionately much broader, the chest is markedly wider in relation to its depth, and the neck is relatively much longer. Of all these proportions the relative chest girth and the relative shoulder breadth show the most striking differences between higher and lower primates and we may assume, therefore, that the most profound evolutionary alterations consist in a widening of the chest and a broadening of the shoulders. In regard to his trunk and neck proportions man stands among adults nearest to the mountain gorilla in two instances, nearest to the chimpanzee in one instance, nearest to the orang-utan in one instance, and nearest to the gibbon in the remaining instance. In none of these proportions does man show an extreme departure from the condition in the macaque; indeed, the human trunk proportions are much more conservative than those of, e.g., the gorilla.

Position of Nipples

Adult man has the lowest placed nipples among all simian primates. The vertical position is accurately expressed by the percentage relation between the distance from the level of the nipples to the upper edge of the pubic symphysis and the trunk height. This index averages 80 in macaques, 84 in gibbons, 90 in orang-utans, 86 in chimpanzees, 82 in gorillas, whereas only 76 in man (Schultz, 1933b, Table 8). The horizontal position of the nipples is shown by the percentage relation between the distance from right to left nipple and the chest breadth. This index averages 40 in macaques, 32 in gibbons, 28 in siamangs, 89 in orang-utans, 52 in chimpanzees, 46 in

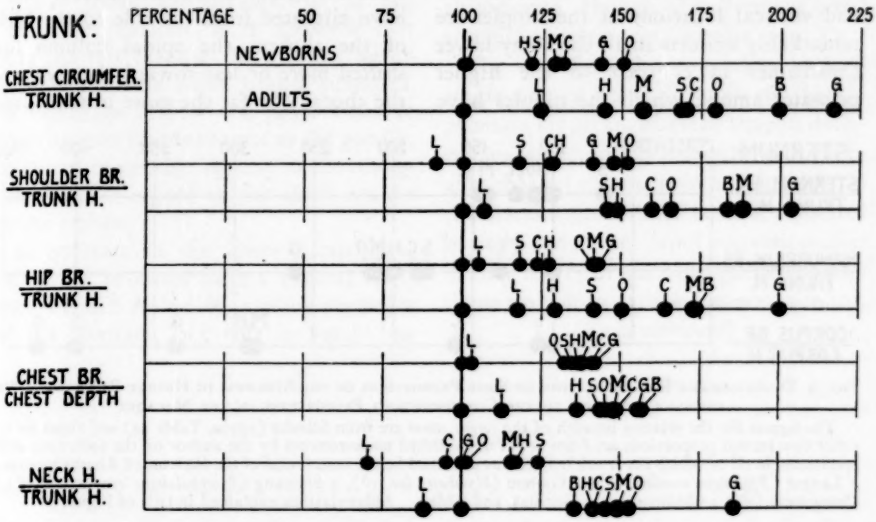

FIG. 8. DIAGRAMMATIC REPRESENTATION OF THE PROPORTIONS OF THE TRUNK AND NECK IN NEWBORN AND IN ADULT HIGHER PRIMATES IN PERCENTAGE RELATION TO THE CORRESPONDING PROPORTIONS IN NEWBORN AND IN ADULT MACAQUE

For each proportion the conditions in newborns are shown on the top line and those in adults on the slightly heavier bottom line. For explanation of abbreviations see title of Figure 7. N.B. The macaque always appears on the perpendicular line "100."

gorillas, and 71 in man. Compared with the conditions in the macaque, the nipples have descended in man (for 4 index units), whereas ascended in the anthropoid apes (for 10 index units in orang-utan); they have moved farther apart in all great apes and man, but this to only a moderate degree in the African apes, to a very marked extent in man, and to the most extreme degree in the orang-utan. It is most significant that the horizontal and vertical locations of the nipples are remarkably uniform in all the many lower catarrhines in contrast to the higher primates among which the nipples have hence most likely phylogenetically. In the quadrupedal catarrhine monkeys the relative shoulder height is very much smaller than in any of the anthropoid apes (Schultz, 1933 b, Table 8).

Sternum

The tremenduous phylogenetic increase in the stoutness of the trunk of higher primates has been associated with many other changes. Thus, the shoulder blades have migrated from the side to the back of the thorax, the spinal column has shifted more or less toward the center of the thorax (by far the most in man), and

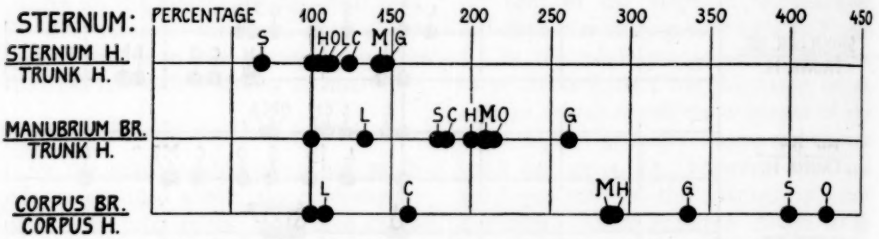

FIG. 9. DIAGRAMMATIC REPRESENTATION OF SOME PROPORTIONS OF THE STERNUM IN HIGHER PRIMATES IN PERCENTAGE RELATION TO THE CORRESPONDING PROPORTIONS IN THE MACAQUE

The figures for the relative breadth of the *corpus sterni* are from Schultz (1930a, Table 14) and those for the other two sternal proportions are from as yet unpublished measurements by the author on the following adult specimens, in all of which the trunk height was measured before maceration of the skeleton: 6 Rhesus monkeys, 1 Langur (*Pygathrix entellus*, ♂), 1 Gibbon (*Hylobates lar*, ♂), 1 Siamang (*Symphalangus syndactylus*, ♂), 1 Orang-utan (♂), 3 Chimpanzees, 3 Gorillas, and 6 Men. Abbreviations explained in title of Figure 7.

shifted in widely differing degrees and even in opposite directions.

Height of Shoulders

In all the anthropoid apes the shoulders lie high above the suprasternal notch, so that the clavicles diverge upward. The chimpanzee possesses the most extreme, average, relative shoulder height, even though it is not nearly as pronounced a brachiator as the Asiatic anthropoids. In contrast to this, the clavicles of adult man are practically horizontal in a position of rest, i.e., the shoulders have descended to the level of the upper end of the sternum and this ontogenetically and the sternum and the pelvis have followed by the increase of their transverse diameters the widening of the entire trunk.

Some of the generic differences in the proportions of the sternum are shown in Figure 9. The total height of the sternum (*manubrium* + *corpus* height) in relation to the height of the trunk differs comparatively little in the higher and in the lower catarrhines, though in man and gorilla the sternum is relatively longer and in the siamang relatively shorter than in the macaque. The relative breadth dimensions of the sternum are the ones which have become greatly increased in all higher primates in striking contrast

to all the lower catarrhines, so that the former are sometimes referred to as the *latisternal* primates. The breadth of the *manubrium* in relation to the trunk height is more than two and a half times greater in the gorilla than in the macaque and the breadth of the *corpus* in relation to the height of this sternal segment is more than four times as great in the orang-utan than in the macaque. As in the general trunk proportions, so in the sternal proportions, is it apparent that man has not reached the extreme development of some other higher primates. In regard to one of the proportions in Figure 9 man stands nearest to the gorilla, in regard to another nearest to the orang-utan, and in regard to the third nearest to the gibbon.

In contrast to the lower catarrhines, all higher primates have a general tendency toward fusion of various segments of the sternum, but this is much less pronounced in orang-utan and gorilla than in chimpanzee and, particularly, man. In many gibbons and some gorillas and chimpanzees the uppermost segment of the *corpus sterni* fuses with the *manubrium*, whereas in orang-utan and man this occurs at best only in very old age. In regard to the comparatively early fusion of the various portions of the *corpus sterni* man is most closely approached by the chimpanzee, though there remain some significant differences (Schultz, 1930 a).

The very fact, that according to each single one of these features the higher primates are arranged every time in different sequences, makes it appear most probable that all the major representatives of this natural group have become separated in early and rather rapid succession after having inherited the same general evolutionary trends from their common ancestor.

(*To be continued*)

THE PROBLEM OF CYCLOPIA

PART II

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IV. NEWER ASPECTS OF THE PROBLEM OF CYCLOPIA

HAVING considered the question of the prospective significance of the eye-forming areas of the anterior end of the neural plate, the time when the ability to differentiate independently as an eye is first acquired by the cells in that region and the factors influencing the localization of eye-forming potencies, we may now consider the application of these facts to the problem of cyclopia. In this connection the question of the relation between the prospective significance and the prospective potencies of the eye-forming regions remains to be considered. Two possibilities suggest themselves. (1) The eye-forming materials of the neural plate may be rigidly determined, a strict correlation between prospective significance and prospective potency existing. (2) The eye-forming materials as late as the early neural plate stage may constitute a harmoniously equipotential system, any part of which is capable of forming any part of the optico-ocular apparatus.

Equipotentiality of Presumptive Medullary Plate

Spemann and Bautzmann ('27) have shown that until relatively late stages of gastrulation the presumptive medullary plate, particularly in its anterior portions, constitutes a harmonious equipotential system. In each of two eggs of *Triton taeniatus* lateral segments of the eggs were cut off by a section which passed to the left of the midline in one member of the pair and to the right in the other. The two smaller segments and the two larger were then healed together so that eggs lacking a median strip and eggs possessing an excess of median material were produced. Thirty-eight of 46 embryos which lacked median material and which were operated on in stages ranging from the horseshoe-shaped to the slit-like blastopore stage, possessed normally proportioned forebrains and eyes. The remaining cases were too young for a decision to be made, or were necrotic or abnormal. No cases of cyclopia were observed. In many cases the embryos possessing superfluous material showed complete regulation of the anterior end.

So far as the presumptive medullary plate is concerned, the problem is therefore solved. The material out of which the tapetum, retina, optic stalks and chiasma will later differentiate is harmoniously equipotential. Material, the prospective significance of which is to form retina may form other parts of the optico-ocular apparatus and vice versa. It is to be noted, however, that in these experiments the entomesoderm or substrate was also involved and the experiments indicate considerable regulative ability on the part of the ectoderm and, particularly, the anterior part of the substrate. The marked regulative capacities of the latter are also borne out in

experiments of Roux ('88), Lehmann ('26), and Holtfreter ('33a) among others. Since the ectoderm alone from the eye-forming region transplanted from a stage well before the oldest utilized by Spemann and Bautzmann will differentiate into a well formed eye (Mangold, '28) we may assume that the ectoderm alone is harmoniously equipotential.

Recent experiments seem to indicate that the equipotentiality of the eye-forming areas of the neural plate persists as late as the neural plate stage in the amphibia. Adelmann ('29a, b) found that the removal of a median strip about $\frac{1}{3}$–$\frac{1}{4}$ of the greatest width of the neural plate of *Amblystoma* did not prevent the formation of two eyes (figs. 20–22). In the majority of cases (9 out of 12) brain and eyes were regulated to form a harmonious whole. This has been confirmed by Mangold ('31) who found that after the removal of a median strip as broad as $\frac{1}{2}$ the greatest breadth of the neural plate, two eyes of considerable size were formed in 11 of 26 cases and absent in only four (fig. 23). The removal of a lateral third of the neural plate results in the formation of a rudimentary optic vesicle on the operated side, but if the antero-posterior extent of the defect is not great enough an eye of practically normal proportions may be formed (Adelmann, '29a). To prevent completely the formation of an eye the defect would have to extend almost or quite to the midline and back as far as the broadest portion of the neural plate. This is in accordance with the findings of Wachs ('20), who demonstrated, further, that a small eye formed after the removal of a lateral segment of the medullary plate may subsequently attain normal size and structure. A similar restitution was also noted by Mangold ('31). When two-thirds of the anterior end of the neural plate are removed, the remaining lateral third gives rise to an eye which may equal the normal proportions (Adelmann, '29a).

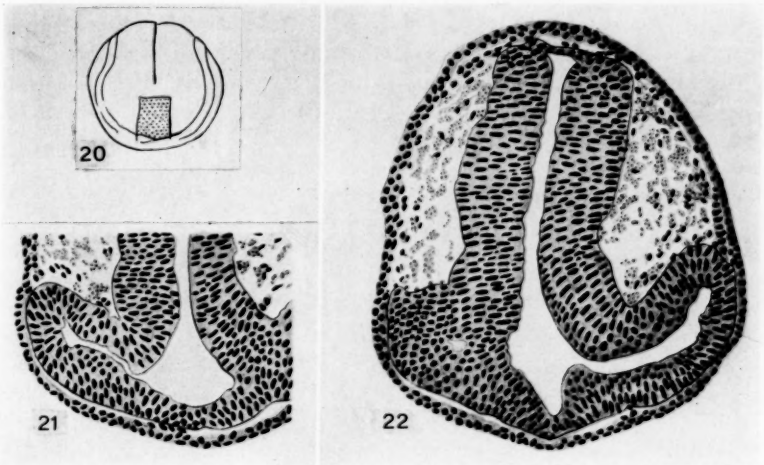
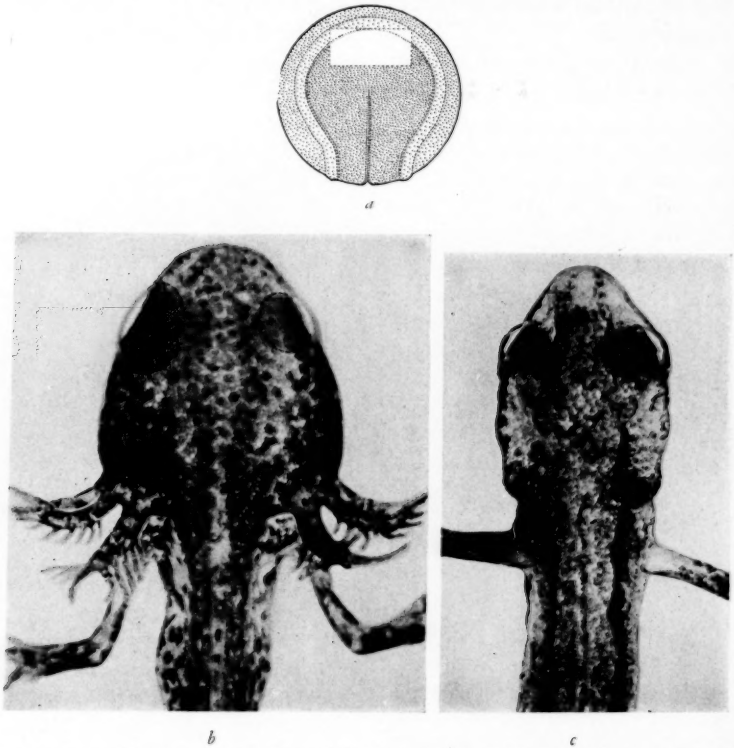


FIG. 20. CAMERA LUCIDA DRAWING OF AN EARLY NEURAL PLATE STAGE OF AMBLYSTOMA PUNCTATUM FROM WHICH A MEDIAN STRIP HAS BEEN REMOVED
The excised area is stippled

FIGS. 21–22. DRAWINGS OF SECTIONS THROUGH THE OPTIC VESICLES OF EMBRYO FIXED TWO DAYS AFTER THE OPERATION SKETCHED IN FIGURE 20. (ADELMANN, '29)

The experiments of Adelmann and Mangold may be contrasted with those of Stockard ('13c) who found that 45 per cent of nine embryos from which a median strip of the neural plate had been removed failed entirely to develop eyes; four others had defective eyes. In 80 per cent of 30 embryos from which lateral portions of the neural fold had been removed, both eyes were formed. The difference may, perhaps, be explained on the basis of age-differences in the material used, variation in the width of the strips removed, or possibly individual differences in the extent of the eye anlage in different strains.

In spite of these differences the experiments of Mangold and Adelmann indicate that the eye-forming potencies of the anterior end of the neural plate are more or less diffusely localized and extend beyond the bounds of the presumptive anlage as defined by Manchot and Woerdeman, a conclusion also reached by Mangold ('28). They demonstrate, further, that cyclopia cannot be produced in the urodele by simple excision of even a relatively broad median area of the neural plate (as great as $\frac{1}{2}$ the greatest width, Mangold, '31) as one might expect if there a strict determination of parts. Both



a *b* *c*

FIG. 23. RESULTS OF THE EXTIRPATION OF A BROAD MEDIAN AREA OF THE NEURAL PLATE IN TRITON TAENIATUS

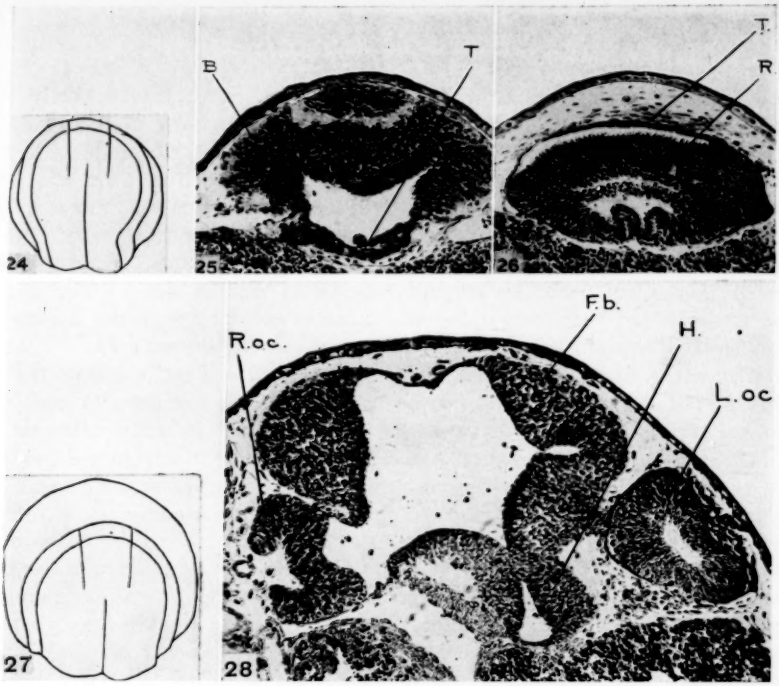
(*a*) A piece $\frac{1}{3}$ of the length and $\frac{2}{3}$ of the width of the cephalic portion of the neural plate is removed. (*b*) Seventeen days after the operation, two eyes are present, the right about $\frac{1}{3}$ the size of the left which is of almost normal size. (*c*) Head of the metamorphosed animal, 103 days after the operation. The right eye has been regulated to almost normal size. (Mangold, '31).

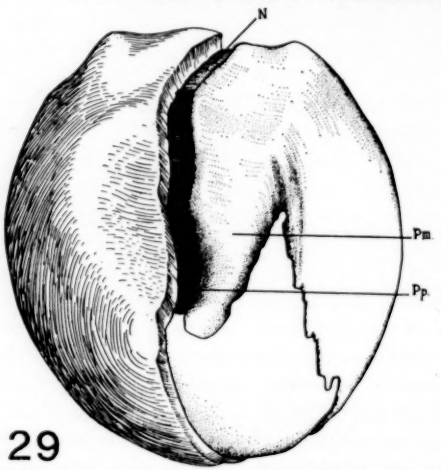
Adelmann and Mangold conclude that in the case of median defects, a regulation between brain and eye, especially in the transverse diameter of the plate, is possible. Daltrop ('32) has recently shown, however, that in the case of lateral defects reaching to the midline, the regulation and restitution of the brain are affected almost entirely by the utilization of material situated caudal to the defect, the material on the normal side aiding only in restoring the dorsal portions of the reconstituted brain. In its ventral portions the intact side is drawn out laterally in accordance with its normal movements. Since, however, the ventral portions of the forebrain, and diencephalon may be replaced by prospective hindbrain material of the operated side, her results do not prove that the ventral parts of the forebrain and midbrain on the intact side lack the ability to replace the ventral portions of their counterparts on the operated side, but that when left in situ their normal shiftings prevent them from doing so. Daltrop's experiments do not prove that in the case of a purely median defect, all of the restitutive tissue comes from the caudal edge of the wound.

Eye-forming Potencies Higher Medially than Laterally

Transplantation of median and lateral areas of the anterior end of the medullary plate yields further evidence as to the properties of the eye-forming materials. In transplants of median and lateral thirds of the anterior end of the neural plate of *Amblystoma*, without the underlying roof of the archenteron, into the belly wall of older hosts, Adelmann ('30) found that over six times as many eyes were differentiated from median as from lateral strips. The eye-forming potencies of the median regions of the neural plate alone are therefore much greater than those of the more lateral regions. The median strips in all cases differentiated into perfectly single eyes often resembling cyclopean eyes in their relation to the implanted brain (figs. 24–26). Such eyes are attached to the brain by tapetum and there is an entire absence of any structure which may be interpreted as chiasma. Furthermore the donors of median tissue which differentiated as an eye often possessed a normally proportioned brain and eyes. In one case the donor formed one eye from the right lateral third of the anterior end of the neural plate left in situ, while eyes were formed from both median and left lateral strips when transplanted from the same donor. The experiments as a whole indicate that the various regions of the optico-ocular apparatus (i.e., the primitive chiasma, the optic stalks, retina and tapetum) are not rigidly determined in the neural plate itself in the early neural plate stage of *Amblystoma*. This is especially clear from transplants of median strips in which a single cyclopean-like eye was differentiated from the region where the chiasma and optic stalks were supposed to be rigidly determined. In the past some misunderstanding has been caused by confusion as to the exact meaning of the term 'chiasma.' In early stages the optic stalks are connected across the midline by a strip of tissue, very slender anteroposteriorly and very narrow transversely, lying in the depths of the primitive optic furrow. This may possibly best be referred to as the primitive chiasma. The definitive chiasma is formed later out of and in front of it when the optic nerve fibers invade the terminal ridge of the neural plate. In cyclopia in the absence of optic stalks neither the primitive nor definitive chiasma is formed. Throughout this discussion, 'chiasma' should be interpreted as referring to the primitive chiasma.

Corroborative evidence as to the distribution of the eye-forming potencies of the neural plate and the labile character of the





FIGS. 24–26. RESULTS OF THE HETEROTOPIC TRANSPLANTATION OF A MEDIAN STRIP OF THE NEURAL PLATE WITHOUT THE UNDERLYING ROOF OF THE ARCHENTERON OF AMBLYSTOMA PUNCTATUM

Figure 24, camera lucida drawing of donor. Figures 25–26, photographs of two sections through the brain and single eye which have differentiated from the transplant in the belly wall of the host. *B.*, implanted brain; *R.*, retina of implanted eye; *T.*, pigment layer of same. (Adelmann, '30).

FIGS. 27–28. RESULTS OF THE HETEROTOPIC TRANSPLANTATION OF A MEDIAN STRIP OF THE NEURAL PLATE TOGETHER WITH THE UNDERLYING ROOF OF THE ARCHENTERON OF AMBLYSTOMA PUNCTATUM

Figure 27, camera lucida drawing of donor. Figure 28, section through the brain and two bilaterally placed eyes which have developed from the transplant in the belly wall of the host. *F.b.*, implanted forebrain; *H.*, hypothalamus; *L.oc.*, left eye of implant; *R.oc.*, right eye of same. (Adelmann, '30).

FIG. 29. MODEL (X CA. 30) OF AN AMBLYSTOMA EMBRYO IN THE NEURAL PLATE STAGE SHOWING THE RELATIONS OF THE ANTERIOR END OF THE ROOF OF THE ARCHENTERON TO THE NEURAL PLATE

The ectoderm has been removed on the left side. *N.*, notochordal plate; *Pm.*, mandibular portion of prechordal mesoderm; *Pp.*, prechordal plate. (Adelmann, '32).

localization of its potencies has recently been gathered by Alderman ('35) for an Anuran. He finds that in *Hyla regilla* median rostral squares of anterior medullary plate transplanted to the belly wall of other individuals form single eyes attached to pieces of brain tissue and that the reversal of a median rostral square of medullary plate *without the substrate* results in the formation of brain tissue from presumptive eye and eye tissue from presumptive brain. "Eye determination, contrary to the conclusion of other workers is labile in the neural plate stage." Dragomirow ('32, '34) states that in *Triton taeniatus* the presumptive pigment and retinal layers of the eye are approximately equivalent in their potencies in early stages, the process of determination proceeding centrifugally from a central point corresponding approximately to the central portion of the pars optica. The retinal layer becomes specifically determined at about stage 29, but the pigment layer remains labile for a longer period.

The situation appears to be similar in the chick where Clarke ('34) finds that: (1) eye-forming capacity is present in a band across the blastoderm at the level of the node in streak stages and the anterior end of the notochord in head process stages, (2) there is a medio-lateral gradient in frequency of eye production and in capacity for differentiation, and (3) median strips of less than 84 micra, and therefore relatively few cells in width, from the brain floor of embryos up to the six-somite stage still gave pigmented and sensory layers of the retina. As further evidence, not conclusive in itself but significant in the light of the foregoing, the following findings may be briefly cited. (1) The fact that in "all experiments and in all species of amphibia investigated, fragments of a certain order of size of the eye anlagen of the neural plate and primary eye vesicle are capable of forming a harmonic eye." (2) The fact that the fusion of two primary optic vesicles may form a single eye. (3) The fact that the site of the choroid fissure is not definitely determined in the primary optic vesicle. (4) The fact that atypical differentiation of the optic vesicle into two retinal cups may occur under certain conditions. (5) The fact that the urodelan eye possesses phenomenal regulative and restitutive powers throughout life. The above facts are cited from Mangold ('31) to whom the reader must be referred for references to the literature.

Factors Responsible for Bilaterality of Eyes

If then eye-forming materials as late as the early neural plate constitute a harmonious equipotential system with the potencies more intensely active medially than laterally, the question may be legitimately asked—what are the factors responsible for the normal differentiation of two eyes instead of but a single one? In other words what are the factors responsible for the attainment of the normal bilaterality of the eyes? In view of the profound effect which the roof of the archenteron (entomesoderm, substrate) has been observed to exert on the determination of the nervous system, we naturally look to it for factors possibly influencing the establishment of two centers of eye differentiation.

In order to determine the effect of the substrate upon the differentiation of the eye-forming region of the early neural plate, Adelmann ('30) excised median and left lateral strips of the anterior end of the early neural plate of the same donor and implanted them together with the underlying entomesoderm (substrate) into the belly wall of an older host. At the time of the operation the prechordal portion of the substrate consists of a narrow median strip, one cell layer thick, the prechordal plate, which is at this time still imbedded

in the roof of the archenteron and which extends from the anterior end of the notochordal plate to the cephalic extremity of the archenteron (fig. 29). The prechordal plate is flanked on each side by strips of prechordal mesoderm which are continued forward from the paraxial mesoderm lying on each side of the notochord. The strips of prechordal mesoderm which flank the prechordal plate later form the mesodermal cores of the mandibular arches from which the muscular elements of the arches are finally differentiated. For this reason it is convenient to refer to these as the mandibular portions of the prechordal mesoderm. At the time of operation the substrate thus exhibits a bilateral disposition of its parts occasioned by the characteristic arrangement of the median prechordal plate and the flanking mandibular portions of the prechordal mesoderm. There is however a potential continuity of mesoderm across the midline in the prechordal region for the prechordal plate is later separated from the roof of the archenteron in a caudo-cephalic direction, whereupon it expands laterally and ultimately furnishes bilaterally disposed masses of mesoderm which come to lie predominately dorsal and caudal to the eye and furnish the material from which are formed at least some of the eye muscles and an undetermined amount of mesenchyme of the head, chiefly in the region lying dorsal and anterior to the mandibular arch.

In the removal of the strips of medullary plate above described, the prechordal plate and very slender adjacent strips of the mandibular portions of the prechordal mesoderm were removed and implanted with the median strips of medullary plate, while the more lateral portions of the entomesoderm were removed and implanted with the lateral strips. Fifty-four per cent of the lateral strips transplanted with substrate formed eyes as contrasted with eleven per cent when transplanted without. The substrate evidently reinforces the eye-forming potencies of the lateral regions of the neural plate.

Seventy-two per cent of the median strips transplanted with substrate formed eyes as contrasted with seventy per cent when transplanted without, not a very significant difference. While the median portion of the substrate in the early neural plate stage has little if any 'reinforcing' effect on the neural plate it possibly, even probably, did exert such an effect in early stages, judging from experiments of Spemann, Holtfreter and others.

The substrate does, however, have an interesting effect on the character of the eyes formed from the transplanted median strips. Two distinct eyes separated by ventral brain floor were formed in 47 per cent of the transplants of median strips with substrate, considering only those cases in which eyes were differentiated (figs. 27, 28). An additional 23 per cent formed two eyes, one of which was more or less rudimentary. No such cases were found in transplants of median strips without substrate, when, as previously noted, only single eyes were differentiated.

These results have recently been confirmed and extended for the anura by Alderman ('35) who finds that in *Hyla regilla* median rostral squares of medullary plate transplanted with substrate form paired eyes in seventy-five per cent of the transplants as contrasted with the single eyes formed from similar transplants without substrate. The possible deleterious effect of the separation of the substrate from the medullary plate is eliminated as a factor by the separation of the two before the medullary plate is implanted on top of the substrate. Paired eyes form from these transplants in about the same percentage of cases. Further, median rostral squares of medullary plate under-

bedded with median substrate taken from beneath more posterior regions of the plate do not form eyes. The 90° rotation of median rostral squares of substrate, having as their anterior boundary the inner rim of the transverse neural fold, disturbs the bilateral symmetry of the embryo to the extent that eye formation on the side receiving the eye-inducing substrate is in advance of eye formation on the side lacking it. The rotation of slightly more anterior median rostral pieces of substrate results in partial cyclopia.

The conclusion to be drawn from the experiments of Adelmann and Alderman is, first, that the substrate obviously has a profound effect on the induction of eye-forming potencies, a deduction which, of course, was already clear from experiments of Spemann and others.. But they also indicate that as late as the early neural plate stage the eye-forming materials of the neural plate alone constitute a harmoniously equipotential system, plastic in its potentialities and capable of forming one or two eyes depending upon factors operating during development. While the eye-forming potencies of the neural plate alone are higher in the median region than laterally, the influence of the prechordal substrate is responsible for the establishment of two bilaterally situated centers of eye formation which arise as the material of the anterior portion of the neural plate expands. The conclusions of Adelmann are supported by Mangold ('31) who, in a striking experiment, produced typical cyclopia by excising the prechordal portion of the substrate in *Triton* (fig. 10).

Abnormalities of the Substrate in Cyclopia

In the light of the above, it is natural to speculate whether or not in experimentally induced cyclopia any structural peculiarities of the substrate are to be observed which might be indicative of an alteration of its normal influence upon the neural plate. Adelmann ('29a, p. 276) some years ago called attention to the fact that the prechordal mesoderm is abnormally disposed in many cyclopean embryos. In a later study (Adelmann, '34) of a number of *Amblystoma* embryos rendered cyclopean by lithium treatment, an alteration of the normal bilateral disposition of the prechordal mesoderm was traced to the open medullary plate stage. Already at this time the prechordal mesoderm reveals a massive continuity across the midline with no indications of a division into a median prechordal plate and lateral mandibular portions such as are encountered in the normal embryo (cf. figs. 30, 31). In the notochordal region it was found that the characteristic arrangement of notochord and bilaterally disposed paraxial mesoderm was essentially normal except that the notochord was entirely separated out of the roof of the archenteron, even though the neural plate was widely open and the notochord had attained a degree of separation from the gut equal to that normally observed in embryos of 6–8 somites. The median continuity of the prechordal mesoderm was interpreted as due to a precocious separation of the prechordal plate mesoderm from the roof of the gut just as in the same sense the notochord had been precociously formed. This early continuity of the mesoderm across the midline is reflected later in the abnormal disposition of the muscle masses in the prechordal region with characteristic continuity across the midline (figs. 32, 33). The arrangement of muscle masses in the prechordal region of the older embryos examined agrees closely with that described or figured by a number of other authors (*Salamandra:* Korschelt and Fritsch, '10; Tsuda, '24; v. Querner, '25; *Rana:* LePlat, '19) and resembles the condition described by Wright and Wagner ('34) in otocephalic guinea-pigs.

Accompanying the abnormal disposition of the prechordal mesoderm, there were found all of the typical anomalies of the other organs of the head so characteristic of cyclopia. Aside from the median eye, the most striking feature was the suppression of the normal bilaterality of the telencephalon, which in extreme cases was represented by only a median strip of nervous tissue extending forward from the median optic aperture between the walls of the dorsal thalamus to the rostral end of the neural tube. The diencephalon and the midbrain to a lesser degree were abnormal. The prechordal portion of the pharynx was abnormal, ending blindly a short distance anterior to the notochord with the consequent absence of the oral

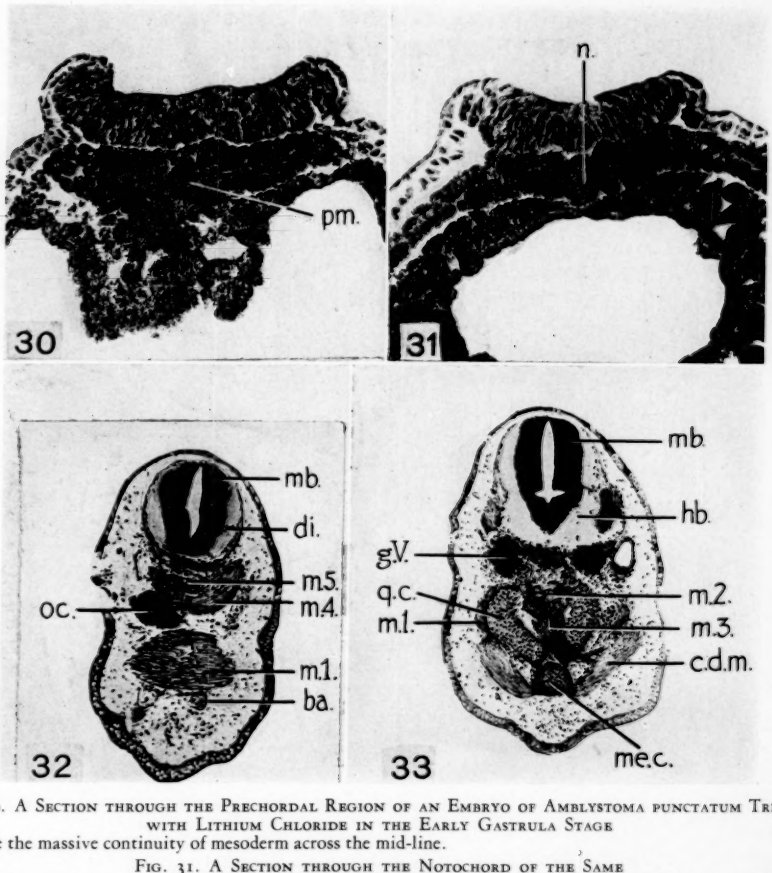


FIG. 30. A SECTION THROUGH THE PRECHORDAL REGION OF AN EMBRYO OF AMBLYSTOMA PUNCTATUM TREATED WITH LITHIUM CHLORIDE IN THE EARLY GASTRULA STAGE

Note the massive continuity of mesoderm across the mid-line.

FIG. 31. A SECTION THROUGH THE NOTOCHORD OF THE SAME

The closure of the neural folds has been delayed but the separation of the notochord from the roof of the archenteron has proceeded to a degree equal to that encountered in normal embryos of 6–8 somites.

FIGS. 32–33. TWO SECTIONS (ARRANGED IN CEPHALO-CAUDAL SEQUENCE) BACK OF THE EYE OF A 12 MM. EMBRYO EXHIBITING CYCLOPIA PERFECTA

Note the continuity of the muscle masses across the mid-line in the mandibular region. *ba.*, balancer; *c.d.m.*, cephalo-dorso-mandibularis muscle; *di.*, diencephalon; *g.V.*, ganglion of the *V* nerve; *h.b.*, hindbrain; *m.1-5*, muscle masses derived from prechordal mesoderm; *mb.*, midbrain; *me.c.*, Meckel's cartilage; *oc.*, 'shaved' portion of the eye; *q.c.*, quadrate cartilage. (Adelmann, '34).

cavity and mouth. The transition to more normal conditions in the differentiation of the prechordal mesoderm was paralleled by more normal conditions in the brain, eye, and olfactory organ.

It was concluded that the correlation between abnormal features of the prechordal substrate and the prechordal regions of the brain supports the idea that the *typical* bilateral differentiation of the forebrain and eye, in particular, normally proceeds under the influence of the prechordal portion of the organizer or 'inducer,' and that cyclopia arising in the period of so-called 'labile determination' is probably due in most cases to alteration of the normal influence of the prechordal portion of the organizer.

Cotronei ('22) had previously noted that in lithium cyclops of *Rana*, the disturbance is primarily localized in the prechordal region, but concluded that lithium acted primarily upon the prechordal portion of the brain which in turn dominated the abnormal differentiation of the prechordal portion of the head. While it is possible that the nervous tissues may be inhibited and that this in turn may exert an influence upon the substrate (cf. Holtfreter, '33a, '33d), the weight of evidence seems to indicate that the suppression of the substrate, in many cases at least, may be the more important factor.

Lehmann ('33) from a less detailed study of chemically produced cyclopean urodeles comes to conclusions similar to Adelmann's. The previously mentioned experiment of Mangold ('31) may also be cited as additional corroboration. Furthermore Raven ('33) describes a case of cyclopia which arose after early implantation of neural crest material which resulted in forcing the substrate away from direct contact with the eye-forming region. Alderman's ('35) experiment in which the rotation of median rostral pieces of substrate results in partial cyclopia may be cited as further evidence pointing in the same direction.

Influence of Substrate on More Caudal Parts of Nervous System

While the exact nature of the influence of the substrate is not yet clear, Holtfreter ('34) reports what appears to be an essentially comparable phenomenon in the differentiation of more caudal portions of the nervous system under various conditions. He states that

> the influence of inductors upon the reacting material is exerted mostly in two directions for which medullary induction may serve as an example. It acts in the first place to determine the material: the ectoderm becomes nerve cells . . . and in the second case it acts as a determiner of form. In order that organ-formation may pursue a normal course, a connective tissue substrate is necessary. This may be explained by a schema (fig. 34) constructed on the basis of many observations. If a piece of medullary tissue which has already been underlain by the substrate and is therefore determined is isolated, it develops further into nervous tissue when floating free (in the medium). Lacking a substrate and modelling influences in its neighborhood it usually rounds up into a sphere, on the periphery of which ganglion nuclei lie, while the nerve fibers course centrally (fig. 34a). If the nervous tissue develops within a mesenchymal mantle, a vesicle or tube with a central lumen is usually formed. The fibers here run centrifugally . . . (fig. 34b). When the neural tube is induced by musculature alone, there always arises, when mesenchyme is present, a tube with an excentrically placed lumen. (fig. 34d) . . . If the medullary tissue is induced by a notochord, the lumen is elongated in slit-like fashion down to the base. If in addition the connective tissue mantle is lacking, the medullary mass remains groove-like (asyntaxia medullaris) and with respect to the distribution of its nuclei behaves like the explant (fig. 34c). But if neighboring tissue (nachbar Gewebe) is present all around it, the medullary mass closes to form a tube which resembles a cross section of the normal spinal cord.

Lehmann ('26) had previously shown the influence of the presence of the notochord on the bilateral massing of material of the neural tube.

The exact nature of the influence, whether chemical, mechanical or both, which has so marked an effect in determining the form of the induced nervous tissue is not clear, but it will be apparent that the influence of the substrate on the normal bilateral massing of the forebrain and eye is possibly of an order similar to that revealed by Holtfreter's experiments, and if so, a uniformity of behavior would exist throughout the central nervous system. It may even be suggested that the typical conformation of prechordal plate flanked laterally by the mandibular portions of the prechordal mesoderm may play essentially the same rôle in determining the typical bilateral massing of materials of the eye and the prechordal region of the brain that the characteristic arrangement of notochord flanked by the somites does in determining the characteristic bilateral massing of material in more caudal regions. In this connection an experiment of Lehmann's ('26) may be cited, in which the removal of the prospective notochord from an early gastrula resulted in the absence of the notochord and permitted the fusion of paraxial mesoderm under the neural tube. In this region the characteristic floor plate of the neural tube was lacking and the typical bilateral arrangement replaced by a basal massing of medullary material.

The rôle of the substrate (inducer) may consist, as Raven ('33) suggests, in serving in some way to "center" the organ anlagen which at first seem generally to be laid down with relatively diffuse boundaries. Raven cites two factors which must be distinguished (1) the formation of the anlage territory and (2) the delimitation of the materials for the organ which probably follows in most cases a centering of the "Organisationspotenz" in a narrowly circumscribed territory. Several possibilities exist: (1) The organ anlagen are laid down "centered" from the first under the influence of the organizer. (2) The organ anlagen are originally diffuse, with approximately uniform distribution of the "Organisationspotenz," the centering occurring autonomously without the coöperation of the organizer.

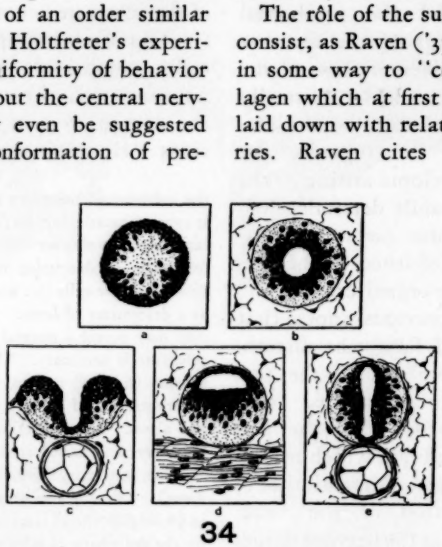


FIG. 34. SCHEMATIC REPRESENTATION OF THE FORMATIVE INFLUENCE OF DIFFERENT NEIGHBORING TISSUES UPON NERVOUS TISSUE

(*a*) Pure culture of nervous tissue. (*b*) Neural tube in the midst of mesenchyme. (*c*) Neural plate induced by notochord only; it remains open but possesses a characteristically thin floor. (*d*) Neural tube with excentric lumen resting upon muscle. (*e*) Normal neural tube resting upon notochord in the midst of neutral neighboring tissue. (From Holtfreter, '34).

(3) As above, but the 'centering' occurs under the influence of the organizer. The last possibility seems best to fit the facts in the present instance, and seems also to fit in with Raven's studies on the inductive capacities of the neural crest.

Influence of Neural Plate

While there is thus experimental evidence that the normal substrate probably plays a large part in determining the typical bilateral symmetry of the neural tube and eye, an experiment of Mangold's ('32) indicates that its place may be more or less successfully taken by the neural plate acting as inducer. He reports the induction of a bilaterally symmetric brain with two eyes by the cephalic third of the right half of the neural plate. We have already noted that the neural plate may induce eye differentiation but the factors responsible for the induction of two bilaterally disposed eyes in this instance are no clearer than they are in the case of the normal substrate. Whether a regulation of the inducing tissues to a bilaterally symmetric structure has preceded the induction and thus influenced the bilateral massing of the induced tissue is not clear. Possibly the implanted medullary tissue furnished the proper mechanical support for the bilateral expansion of the eye-forming materials, a rôle which may also be played by the normal substrate in this connection.

At first it would appear that the induction of secondary embryos by dead organizers and the induction of typical bilaterally symmetric heads by lateral fragments of inducing substances were inimical to the validity of the facts stated above. Holtfreter ('33a), however, has recently shown that such is not the case and has furthermore shown that the materials of the marginal zone have remarkable regulative powers, lateral portions exhibiting regulation and tending to become reconstituted as bilaterally symmetric wholes. Thus a piece of the lateral wing of the presumptive chorda when cultured in vitro differentiated a notochord, bilaterally disposed musculature and at its upper end nervous tissue and epidermis. In addition to bringing further evidence of the existence of regional differences in the action of the organizer in a longitudinal direction, previously adduced by Spemann, he states that the bilateral character of the induction in cases where bilateral heads are induced by lateral portions of the marginal zone

> is conditioned by the fact that the implant itself is first bilaterally regulated and as such induces symmetrical brain structures. This very tendency of a partial organizer when transplanted to complete itself as a more or less integral whole, either from its own substance or by the incorporation of host material, is, indeed, the principal characteristic of the transplanted partial organizer. Thereby it will always be distinguished from a dead organizer. (Holtfreter, '33a, p. 428).

In this connection, however, it must be clearly understood that while the cyclopean head is characterized by an atypical bilaterality or massing of its parts, it is, nevertheless, bilaterally symmetric.

Induction of Cyclopia by Abnormalities of Substrate

The facts drawn from various quarters then seem to favor the view that cyclopia may in many cases owe its genesis to an alteration of the influences normally exerted by the prechordal portion of the substrate upon the normal bilateral massing of the tissue of the eyes and prechordal region of the brain. In this light furthermore, we find a simple explanation of many facts heretofore difficult to explain. Thus, the results of Spemann's ('01–'03) constriction experiments are probably due to the fact that the pre-

chordal region of the inductor was subdivided, resulting in the formation of two heads. Whether cyclopia results or not would depend upon the degree to which the inducing material is able to regulate. His reversal experiments also find a simple explanation, the reversal of the substrate together with the medullary material being responsible for the result. As previously noted, Alderman ('35) finds that reversal of a segment of the early neural plate without substrate results in the formation of eye from presumptive brain and vice versa.

This explanation is also in harmony with the results obtained in the production of cyclopia by the alteration of various environmental factors. It is a well known fact (Bellamy, '19, '22; Woerdeman, '33) that the dorsal lip of the early blastopore where the prechordal region of the organizer is situated before invagination, is the site of intense metabolic activity. Since, as the evidence seems to indicate (Child, '28; Stockard, '21), adverse environmental influences act most vigorously upon whatever regions happen to be metabolizing most actively at the time of their action, and since cyclopia is produced only when embryos are adversely affected by chemicals or otherwise in the early stages of gastrulation when the prechordal portion of the organizer is not yet invaginated, the chances of its being adversely affected would be great. The work of Adelmann and Lehmann shows that a deleterious effect upon the substrate, as reflected in its abnormal differentiation, may actually be demonstrated in cyclopia, in which case, however, its eye inducing ("material bestimmend," Holtfreter) powers have not been destroyed but its form-determining ("formbestimmend," Holtfreter) influences have been impaired. In case the action of the inhibiting agent has been so severe as to destroy entirely the eye-inducing properties of the substrate, anophthalmia would be the expected result.

It has been noted that in cyclopia the typical bilaterality of the parachordal region of the body has not been disturbed by the action of lithium in contrast to the rather striking suppression of bilaterality in the prechordal region. The explanation is possibly to be found in the fact that a potential continuity of mesoderm across the midline exists in the prechordal region, since the prechordal plate, itself prospectively mesoderm, forms a median area of prospective continuity between the more laterally situated mesoderm. In prosectively more caudal regions, however, the mesoderm is separated medially by the notochordal plate and it seems logical to assume that in the latter region there exists a more strongly impressed inherent bilaterality than in the prechordal region.

Cyclopia without Abnormalities of Substrate

It would be rash to assume, however, that the action of adverse environmental factors is always exerted on the entomesoderm (substrate) alone. Stockard ('09b), LePlat ('19), Cotronei ('22), Wright and Wagner ('34) among others, assume that the action of adverse environmental factors is exerted entirely on the medullary plate. In the final analysis, the form and relations of the cyclopean eye and brain are an expression of abnormal developmental behavior on the part of the anterior end of the neural plate and tube. The normal bilateral growth, expansion and differentiation of the latter appear normally to be related to influences arising from the normal organismic environment of the medullary plate (in particular the dorsal lip of the early blastopore or the anterior end of the roof of the archenteron); its failure to occur appears in many

cases to be related to abnormal influences arising within the organism. It is, therefore, logical to infer that abnormal conditions prevailing in the external milieu, by acting directly upon the neural plate may produce essentially the same result.

It should, of course, be clearly kept in mind that, as Mangold ('31) points out, the end result is a product of the reaction of two materials, the substrate and the neural plate, which may be affected separately or in combination (See also Lehmann, '34). It is, indeed, likely that the neural plate may itself be so adversely affected that it is unable to respond typically to formative influences arising from the normal substrate, and we may occasionally expect to find cyclopia or even anophthalmia arising in conjunction with more or less normal differentiation of the substrate. But, on the other hand, normal differentiation of the substrate does not necessarily mean that it has exerted its normal influence on the material and morphological differentiation of the nervous system. Again, the neural plate may be able to overcome to some degree abnormal influences exerted by the substrate. This would naturally depend upon the degree of determination attained by the neural plate and its subdivisions and would probably vary in different species. Consequently normal or almost normal development of the eyes may be expected to be found in some forms although the development of parts derived from the substrate is more or less atypical. Otocephaly, for instance, need not necessarily be accompanied by cyclopia. It is possible, however, that the suppression of the jaws and mouth in these cases may have occurred after the eye-forming material had been determined.

Cotronei ('22) who accepts a rigid determination of the eyes in the neural plate believes that lithium and other similar environmental agents affect the prechordal region of the neural plate primarily and inhibit its normal expansion and growth. He also assumes that the prechordal neural plate directs the differentiation of the rest of the head and results in the establishment of the other cranial anomalies of cyclopia. The lack of expansion of the prechordal brain results in the fusion of the two rigidly determined eye-forming areas because of lack of space to expand. There is undoubtedly some truth in his contention. Before the appearance of the dorsal lip of the blastopore in amphibia an area of heightened metabolic activity in the region of the animal pole, in the region of the presumptive neural plate has been demonstrated by Bellamy ('19), and Holtfreter ('33d) has shown that the induced material in turn reacts upon its substrate. Further, it is undoubtedly true that to a large extent the characteristic pattern of growth and expansion of the prechordal brain determine in large part the pattern of the head (see Kingsbury and Adelmann, '24), but it is still uncertain to what extent these are secondary factors normally set in action initially by the substrate. Guareschi ('34) has recently attempted to substantiate the interpretation of Cotronei by a combination of the use of vital dyes and the action of lithium. After staining median and lateral areas of the prospective eye-forming region, the eggs were treated with lithium solutions and cyclopia induced. The stained eyes were then studied in the gross specimens and it appeared that the cyclopean eye was always stained the color of the lateral areas of the neural plate. He concludes that the two eyes have fused by displacing median material. However, before his interpretation can be accepted, the work will have to be repeated by the study of the dye in sections. His figure 32,

furthermore, clearly shows a blue median strip in the cyclopean eye derived from the stained median area of the gastrula.

Other Abnormal Features of the Cyclopean Head

For the moment the possibility that an inhibition of the normal reactions of the medullary tissue may in some cases be the initiating factor may be set aside in favor of that possibility which seems better to fit the majority of cases, namely an early inhibition of the prechordal region of the substrate. On this basis we may proceed to examine some of the other typical abnormal features of the cyclopean head. This assumption, for instance helps to explain the frequent association with cyclopia of anomalies of the jaws (otocephaly) and mouth; an inhibition of the prechordal substrate as expressed in a suppression of its bilaterality accounting for the fusion of the muscle masses in the mandibular region. Wright and Wagner ('34) in their study of otocephalic guinea-pigs, many of which were cyclopean, believed that all of the abnormalities which they encountered could be traced to a small number of centers—in usual but not invariable order of frequency of defect —ventral mandibular arch, fronto-nasal process, olfactory placodes and cerebral vesicles, median optic rudiment, progressively posterior parts of the brain, dorsal portion of the mandibular arch and hyoid arch. They advance the hypothesis that the basic factor in this class of abnormalities is inhibition of the anterior medullary plate and associated ectodermal placodes, and that one of the effects of such inhibition is interference with the formation and migration of the neural crest. To the failure of the neural crest to migrate they attribute the abnormal formation of the skeletal elements of the jaw and to this in turn the abnormal disposition of the muscles. However, in the cyclopean urodeles of Adelmann and Lehmann, atypical features of the prechordal substrate were detected before the neural crest normally migrates and it would seem more likely that the abnormal disposition of the prechordal mesoderm had determined the abnormal conformation of the derivatives of the neural crest. From the order of frequency noted by Wright and Wagner ('34) it would appear that the prechordal mesoderm was more vulnerable than the neural plate. However, it must be kept in mind that a relatively late suppression of the mandibular arches would result in otocephaly as will be apparent from the figures of Streeter ('22) and in this case cyclopia would not be expected to accompany it.

The median massing of the prechordal mesoderm in *Amblystoma* seems to effectively prevent contact between the pharynx and the presumptive oral ectoderm, thus accounting for the absence of the oral cavity in many cases. We know from the work of Adams ('24) and Ströer ('33) that the oral ectoderm depends upon contact with the pharynx for its normal differentiation.

Adelmann ('34) found further that the arrangement of the prechordal mesoderm in cyclopia often prevents contact between the brain floor and ectoderm in the hypophyseal region, which in connection with Blount's ('32) finding that the differentiation of the anterior lobe of the hypophysis depends upon contact between brain and ectoderm seems to explain the absence of the anterior lobe of the hypophysis in many cases.

The singleness or doubleness of the olfactory sac of cyclopean *Amblystoma* embryos was found to be correlated with the degree of typical bilateral differentiation attained by the prosencephalon, and it appears likely that inductive activity on the part of the latter is responsible for

the result. Raven ('33) reports a case in which supernumerary olfactory organs were apparently induced by splitting of the anterior end of the brain. In cyclopia perfecta, due to the suppression of the typical bilaterality of the forebrain, but one olfactory placode is induced.

In adopting this approach, however, we must not be deluded into imagining that the problem of the harmonic development of the cyclopean head is a simple one. While at present it would appear that the end result is largely determined by the balance struck between the reacting material of the neural plate and ectoderm and the inducing material of the substrate which may, as we have supposed, be affected separately or in combination, the final picture is, however, no doubt influenced by a complex of factors not yet clearly identified. In its normal development the head exhibits what may be designated, for want of a better term, a certain 'wholeness' or unity, comparable to that exhibited by the organism as a whole. It is achieved by and is an expression of a delicate balance between the various parts of which it is composed and correlative adjustment in the development of the subordinate parts which in turn make up larger units. Thus Dragomirow ('33) describes a coördination of 'partial processes' operating within the eye itself and no doubt a similar situation exists in the case of the other organs of the head. The harmonious development of the normal head is thus brought about by the harmonious coöperation of a number of factors most of which are still obscure. The harmonic development of the cyclopean head will only be completely understood when the nature of some of these more obscure processes is better known.

V. SUMMARY

From the foregoing we see that the controversy as to whether the "eye enlage is primarily median and single or not" has largely lost its point and becomes in part a matter of definition. Under the influence of the roof of the archenteron there is probably at first established a diffusely localized, homogeneous or harmoniously equipotential 'eye-field.' On this the substrate normally acts further to establish two bilaterally situated centers of eye-formation. But as late as the early neural plate stage, in amphibia at least, they are not rigidly determined and the eye-forming materials of the gastrula and of the early neural plate should be regarded as potentially either single or double, the outcome depending upon factors operating during development.

Finally, in order that a clearer differentiation can be made between "Observation and Reflection" than has been possible in the preceding pages, it may be wise to state what seem now to be the established facts.

(1) The localization of eye-forming potencies in the appropriate region of the anterior end of the neural plate normally occurs under the influence of the roof of the archenteron (Spemann, '31; Mangold, '28; Holtfreter, '33a, '34; *et al.*).

(2) The substrate (entomesoderm) determines not only the differentiation of the ectoderm as nervous tissue but also its morphology (Holtfreter, '34).

(3) The presumptive or prospective eye anlage, comprising the materials for both eyes, occupies a median territory of the anterior neural plate measuring but $\frac{1}{3}$–$\frac{1}{4}$ of the greatest diameter of the plate. The materials for the eyes are separated anteromedially by material whose presumptive significance is to form a part of the lamina terminalis and connected (or separated?) posteriorly by a narrow zone of material normally involved in the formation of the primitive chiasma (Manchot, '29; Woerdeman, '29).

(4) The eye-forming potentialities of

the anterior end of the neural plate are diffusely localized (Adelmann, '29; Mangold, '31) and so far as the neural plate alone is concerned are harmoniously equipotential, any portion being able to form any part of the optico-ocular apparatus (Adelmann, '30).

(5) Eye-forming potencies are higher medially than laterally (Adelmann, '30; Clarke, '34).

(6) The bilateral differentiation of two eyes from the relatively plastic eye-forming materials of the neural plate normally depends upon influences exerted by the underlying entomesoderm (Adelmann, '30; Holtfreter, '33a; Alderman, '35).

(7) In cyclopia atypical differentiation of the prechordal substrate often occurs, the degree to which the substrate is abnormally disposed is correlated in particular with corresponding degrees of abnormality of the brain and eyes (Lehmann, '33; Adelman, '34).

(8) Cyclopia may be produced by excision of the prechordal portion of the roof of the archenteron (Mangold, '31).

In the light of the foregoing, we have attempted in the preceding pages not to 'explain everything' in connection with cyclopia for we realize that the situation is complex and that the problem is far from solved, but to present consistently a line of thought or point of view which we think is interesting and suggestive, and which we hope will be stimulating.

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ABERRANT FEEDING BEHAVIOR AMONG INSECTS AND ITS BEARING ON THE DEVELOPMENT OF SPECIALIZED FOOD HABITS

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THE behavior of insects with relation to food is extremely diverse if we consider them as a group. Any survey of its component parts reveals at once a more or less orderly distribution of the several types of food-habits with reference to characteristic peculiarities of structure, development and instinct. The dependence of trophic behavior upon the adjustment of such intrinsic factors to the environment is obvious, and we must look for any indications of the origin and development of predatism, vegetarianism, parasitism and the like by inquiry into the interactions of these internal and external modifications.

Diversity in behavior among insects is readily traceable to their extremely plastic structural organization which admits of many drastic changes in the form of bodily parts, such as the mouthparts, legs, respiratory system, wings, etc. Such structural peculiarities frequently appear without associated modifications in other structures and correspond almost invariably to changes in habits to which they are highly, often exquisitely adapted. Whatever theoretical interpretation we may apply to the origin of these adaptations, their occurrence is real and by no means infrequent. Many cases of peculiar food-relations appear to be primarily of this nature.

The indirect development of the higher insects opens new avenues for the initiation of profound although transitory structural modifications in the nymphal and larval stages, since the latter are interpolated in such a way that they may develop at this time entirely novel characteristics which leave no impress upon the imago.

The writer has previously dealt at some length with many of these phenomena and the reader is referred to this earlier paper (The Classification of Insects with Reference to the Characters of the Larva and Pupa) published in the *Biological Bulletin*, vol. 37, pp. 1–21 (1919).

Similarly, hypermetamorphosis, which is particularly associated with developmental changes in food-habits, results in a differentiation of even the several larval stadia into divergent types, and quite independently of one another. Thus the food relations of a single individual may pass through several distinct, often radically different phases, each adapted to the requirements of life at a particular time.

The part played by modifications of instinct is the most difficult to comprehend, yet these continually intrude as a subtle background in any picture we may form of the food-habits of an insect. Here indeed, instinct appears frequently to transcend any materialistic considerations, at least of the kind which we as humans apply either to the epicurean selection of food, or to its choice on a nutritional basis.

As I believe that the account included on the following pages throws some light on the rôle of instinct in this connection,

it seems best to defer any more detailed statement until this material has been presented.

The food-habits of most insects as well as other animals fit quite readily into some one of the types that are inscribed at the four corners of the accompanying chart (Fig. 1). There always remains a residuum of forms which do not fall decisively into any one group; some of these combine more than one type, as phytophagy and saprophagy; some may be regarded as predators or parasites, dependent upon our exact definition of these two terms; others may pass from one to another during ontogeny; and again some are so highly specialized that although easily excluded from three categories they still differ quite fundamentally from the typical representatives of the remaining group. Finally the four types are not entirely coördinate in extent or range. By and large, however, they serve very well for most purposes of comparison and each includes a wide series of insects.

On our chart the sequence of these four types is: Saprophagy, Phytophagy, Predatism and Parasitism. It would be difficult to present any conclusive evidence to prove that any one of the first three is more primitive than the others although I believe that the order given is probably correct at least for the terrestrial winged insects. In the case of the amphibiotic orders with aquatic nymphs like the mayflies and stone-flies it is quite possible the earliest forms were entirely sapro-

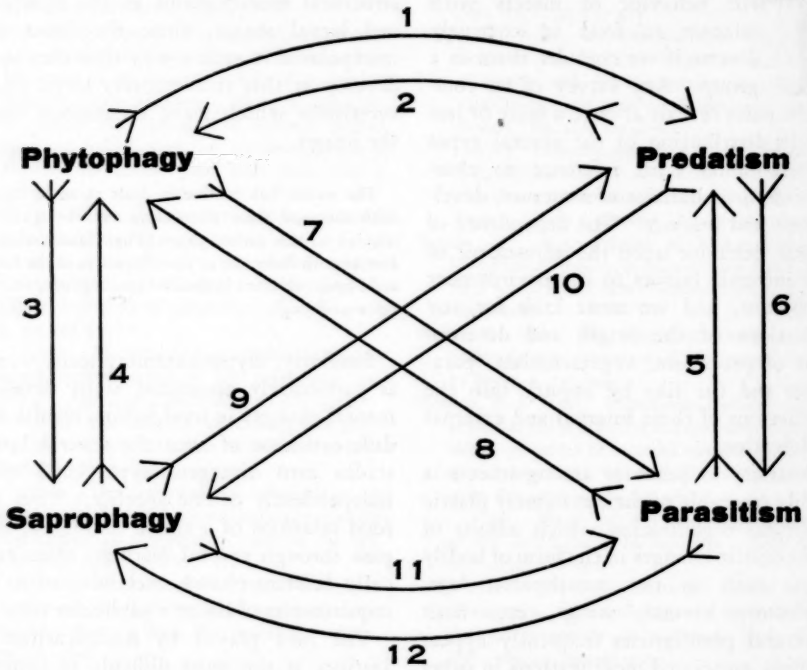

FIG. 1. DIAGRAM OF CHANGES IN FOOD HABITS

phagous. Since primitive types of both these series like the mantids and dragonflies are predatory this method of feeding undoubtedly arose very early in the history of insects. However, since the food of such insects consists mainly of other insects, predatism in its present form must represent a derived method of feeding.

Among living insects several orders are preëminently phytophagous and several are entirely or generally predatory. Parasitic and saprophagous forms are more commonly restricted to smaller groups, usually superfamilies or families, and one type or another frequently appears in a small part of a group where it is otherwise unknown. Thus among Lepidoptera, the caterpillars are constantly vegetarian, except for a few genera that have become carnivorous or predatory. Again in the several superfamilies that form the parasitic Hymenoptera a few scattered forms have adopted a purely vegetarian diet. The more closely we examine the food habits of insects, the more evident does it become that many shifts of this nature have occurred. These often represent quite complete reversals of habit and they are not generally connected by intergrades with the habits of the groups from which they have undoubtedly arisen. Once such a change has occurred, the new habits show the same remarkable constancy that characterizes the food-habits of insects in general.

I have indicated by arrows on the chart the shifts which may occur when any species changes from one method of feeding to another and it will be seen that twelve ways are possible between the four designated types. It is a simple matter to recall numerous instances of most of these possible shifts, although some occur much more frequently than others.

With these generalized statements before us, we may enquire more closely into some specific cases which illustrate such shifts or sudden changes in food-habits. To avoid any doubt or ambiguity as to facts, care has been taken to disregard any observations that are not fully authenticated, however probable their accuracy may be, and furthermore, for the sake of brevity only four of the aforementioned twelve types of shifts are dealt with.

I. CHANGE FROM PHYTOPHAGOUS TO PREDATORY HABITS

The Lepidoptera probably furnish the best example of predatory habits arising in a few scattered members of an enormous group of insects where the larval stages are almost uniformly vegetarian. These sudden shifts in food-habits are still more remarkable when we recall that the diet of the phytophagous types is commonly greatly specialized by restriction to particular food-plants.

The following very brief account includes a summary of the habits of some of the Lepidoptera which have renounced the vegetarian habit to become carnivorous. In numerous instances there remain details yet to be elucidated, and undoubtedly many additional cases will be discovered as the life-histories of the Microlepidoptera become better known.

The larvæ of a number of butterflies are known to be predatory or at least highly carnivorous. These are very generally distributed throughout the world, but all belong to a single family, the Lycænidæ. Two subfamilies (Gerydinæ and Lipyrinæ) probably contain only carnivorous species, while a few members of another (Lycæninæ) lose the vegetarian habit characteristic of the remainder of the family only during the last larval instar. Thus a comparatively small group of butterflies exhibits very clearly a complete shift from plant to animal food. The habits of these

aberrant forms are summarized by Clark ('26) in a very complete paper from which many of the following notes have been drawn. Although a knowledge of carnivorous habits in any butterfly larva dates back scarcely half a century, the observations of many entomologists (1) have been required to accumulate the still meagre information now available. (The numbers in parentheses refer to the sections of the classified list of literature at the end of the paper.) The food-habits of ten genera and about fifteen species are at least fairly well known and these show very considerable diversity. In all cases there is a rather clear association with either Homoptera (Coccids, Aphids, Treehoppers or Leaf-hoppers) or with Ants, or more usually with both Homoptera and ants. The latter type of biocœnosis really represents the addition of the lycænid caterpillar to the more familiar and widespread association of ants with Homoptera. From the known facts it is not easy to determine, however, just how the peculiar relations now existent have arisen. Since many caterpillars of the strictly phytophagous Lycænidæ have frequently been observed to show strong cannibalistic tendencies we may infer that this led to the adoption of carnivorous habits in forms that feed upon aphids or coccids. One of these is the North American *Feniseca tarquinius* whose larvæ live in colonies of *Schizoneura tessellata* on alder and in those of similar woolly aphids on other plants. Similar relations exist in the genus *Spalgius*, of which an Indian species, *E. epius* and also an African one, *E. lemolea* feed on mealy-bugs (*Pseudococcus*). As these aphids and mealy-bugs are regularly attended by ants it is but another step to a more intimate association with those ants which regularly build shelters over Homoptera. This is illustrated by several African species, *Megalopalpus zymna*, *Aslanga vininga*, and *A. lamborni* which feed on leaf-hoppers, treehoppers and lecanioid coccids. In an Australian form, *Liphyra brassolis*, the caterpillars have become myrmecophagous, living in nests of the fierce tree ant, *Œcophylla* on whose larvæ they feed, apparently accepted rather unwillingly by the ants but partially protected by their slug-like form and scuted integument. Finally a symphilic type of myrmecophily appears in an African form, *Euliphyra mirifica* in which the caterpillar has developed a snout-like head, which is thrust into the ant's mouth demanding food. This is forthcoming, although only in small quantities, necessitating a rather prolonged period of larval growth.

Among the carnivorous Lycænidæ there still remain certain forms, such as two British species of *Lycæna* (*L. arion* and *L. alcon*) which are vegetarian as young caterpillars, but enter the nests of ants during the last larval instar where they become carnivorous and feed on the larvæ of the ants. In their later stages these caterpillars are provided with honey glands and are attended by ants even before they enter their nests. This type does not appear to be derived from the series mentioned previously and must represent an independent development of carnivorous habits.

In all the carnivorous lycænid caterpillars noticeable structural adaptations occur. Those in members of the first group involve great modification in body form or a thickening of the cuticle, and in the second group they are restricted mainly to the development of special glands like those occurring in various other myrmecophiles. It is noteworthy also that the adult butterflies of some of the carnivorous lycænids feed upon honey dew secreted by the same species of aphids that are eaten by their larvæ.

Similarly, among several other families of Lepidoptera the predatory habit appears in the caterpillars of a number of moths, mainly of the tineoid series. The erratic distribution of these cases with reference to taxonomic affinities indicates at once that we have to deal with the independent origin of this habit in several unrelated groups. The caterpillars of one entire family, the Epipyropidæ (2) are, so far as is known, all carnivorous, feeding on various Homoptera (Jassoids, Fulgoroids and Scale Insects) and usually remaining attached to the body of the host during their entire period of growth. The head and mouthparts are much modified for sucking the juices of their prey and as the family enjoys a wide distribution in India, Japan, Australia and both Americas, predatism here is undoubtedly of long standing. This view is further substantiated by the incipient hypermetamorphosis, as the larva is more or less campodeiform when hatched, but later degenerates into an inactive, hemispherical grub.

In North America the caterpillars of several small moths feed on coccids (3). *Euclemensia bassettella*, an aberrant member, of the tineoid family Heliodinidæ is a common enemy of the large oak-infesting, gall-like coccids of the genus *Kermes*, feeding within the body of its host (Comstock, '81; Hollinger and Parks, '19). *Holcocera iceryaella* of the family Blastobasidæ, which similarly attacks various coccids in California, is thought probably to feed to some extent (Essig, '16; Basinger, '24), on dead specimens, wax-scales, etc. In India a species of *Holcocera* (*H. pulverea*) feeds on lac, affecting both living lac insects and stored lac (Ramakrishna Ayyar, '29). In India and Australia, Heliodinidæ (Fletcher, '20; Tillyard, '26) of the genus *Strathmopoda* are coccidivorous, although the genus contains also vegetarian species in both these regions, and in India the related *Œdematopoda* includes both predatory and phytophagous forms. In one Australian species of *Strathmopoda* the food consists of the eggs of spiders, recalling the North American *Dicymolomia julianalis* (Gahan, '09; McCreary, '30) belonging to still another family (Pyralididæ) whose larvæ feed on eggs of the bagworm (*Thyridopteryx*), each caterpillar invading the larval case of the bagworm that contains the egg mass of the host. In the same family, Pyralididæ, an Indian member of the Phycitinæ (*Phycita dentilinella*) is carnivorous, feeding on pupæ of a Eucleid moth as well as those of a wild silkworm, *Cricula trifenestrata* (Ramakrishna Ayyar, '29).

The Noctuidæ also contain at least two well known genera with carnivorous habits. These are *Eublemma* which contains numerous Indian species that feed on scale insects of various kinds, and the Australian *Catablemma* (Froggatt, '10; Tillyard, '26) with similar habits. In connection with the predatory habit in this family it is interesting to note that its members seem to be especially prone to exhibit cannibalistic tendencies (Berg, '92; Brues, '20; Lommatsch, '26; Moore, '12), although this phenomenon is by no means restricted to them.

Perhaps most remarkable among the predatory lepidopterous larvæ is *Cyclotorna*, sole representative of the peculiar Australian family Cyclotornidæ. Five species are known from Queensland (Dodd, '12), several of which, and probably all, are predatory on leaf-hoppers during early larval development and later feed on the larvæ of ants. In the case of *Cyclotorna monocentra* as discovered by Dodd, the eggs are deposited on the twigs of trees and the young larvæ feed by attaching themselves to the bodies of nymphal jassids which are present on the trees. The larvæ remain

active and may shift from one host to another; after a period of growth they spin a silken cocoon from which the caterpillar emerges after having undergone some changes. This caterpillar then induces a worker of the common ant, *Iridomyrmex purpureus* which frequents the trees where the jassids occur, to carry it to the ant's nest. Here it completes its feeding at the expense of the ant-larvæ. It thus appears probable that the caterpillar is predatory during its entire development, as its behavior on the jassids does not suggest that it feeds upon the sweet secretions which serve to attract the ants.

A survey of predatory habits might be extended into other groups that are primarily vegetarian as many such have often been observed, but they are quite similar to those just mentioned. It is, however, of interest to find that the Orthoptera (*sensu stricto*), which are much less highly specialized with reference to food than the Lepidoptera, show comparable digressions. This has been repeatedly noted in various parts of the world among the long-horned grasshoppers of the family Tettigoniidæ (Locustidæ), particularly members of the Conocephalinæ (Xiphidiinæ) (4). In North America species of *Orchelinium* have been observed to eat beetles, moths and other Orthoptera and in Hawaii *Chonocephalus* commonly feeds on leafhoppers, mealy-bugs and pupæ of moths. In Natal, caterpillars of a stalk-borer (*Busseola fusca*) are frequently eaten by a related grasshopper (*Clonia vittata*). Even certain wingless Stenopelmatidæ, as *Udeopsylla nigra*, readily consume may-beetles, other Coleoptera and grasshoppers.

Among the Orthoptera these aberrant habits are less firmly fixed than they are in most Lepidoptera as a vegetarian diet is only supplemented by animal food at times, occasionally to such an extent that plant food may be practically eliminated. As cannibalistic tendencies are here often evident and as the prey frequently consists of related Orthoptera, it is not surprising to find this taste for animal food, particularly as the mouthparts are unusually well adapted for the purpose in the Conocephalinæ, to which most of the records relate.

Turning to a more specialized order like the Hymenoptera where the lower forms are phytophagous, carnivorous aberrations frequently occur among adult sawflies. This is attested by numerous observations (5) of these insects, which are known to capture and eat other kinds of insects.

II. CHANGE FROM PREDATORY TO PHYTOPHAGOUS HABITS

The appearance of phytophagous habits in a family of typically predatory insects is well exemplified by the Coccinellidæ (6), an extensive group of small beetles. With the exception of one very discrete series, these insects subsist almost entirely on other insects that are devoured by larvæ and adults alike. Disregarding for the moment two minor groups and a few scattered cases, the phytophagous forms, which represent without doubt the derived type, form a subfamily, Epilachninæ. Our present knowledge of their food-habits is confined to certain representatives of the large, cosmopolitan genus *Epilachna* and of two related genera, *Subcoccinella* and *Cynegetis*. They are purely vegetarian and show the same specificity in choice of food-plants that is characteristic of other phytophagous beetles, such as the Chrysomelidæ. The habits of about fifteen species are well known through the observations of numerous entomologists (Del Canizo, '28; Chue, '30; Den Droop, '18; Fletcher, '14; De Fonseca and Autuori,

'31; Friend and Turner, '31; Froggatt, '21; Howard and English, '24; Klemm, '29; Korschevsky, '29; Krishnamurti, '32; Murum tsu, '19; Schilder, '28, '29; Stroubal, '26; Subramaniam, '24; Takagi, '32; Tanabe and Sekiya, '31; Veitch, '31) as some are economically important pests in both the New and Old World.

In North America we have two abundant species of *Epilachna* one of which, *E. borealis*, feeds mainly on the foliage of our native wild cucumber, *Echinocystis lobata*, but also commonly affects certain introduced cucurbits in gardens such as squash and pumpkin. The other, *E. corrupta*, which has recently extended eastward into the Atlantic States from the Southwest, is known as the Mexican bean-beetle since it feeds generally on various beans and more sparingly on some other leguminous herbs. In Europe two common forms, *E. chrysomelina* and *E. undecimmaculata* occur on cucurbits, the latter generally restricted to native species of *Bryonia* and *Echallium*. No European species of *Epilachna* is known to attack beans or other Leguminosæ, but the related *Subcoccinella vigintiquatuorpunctata* feeds regularly on alfalfa, and sparingly on certain other unrelated plants of several families, *e.g.*, *Saponaria*. In Europe another food-plant appears in the dietary of *Epilachna*, for *E. chrysomelina* sometimes appears abundantly on potato foliage when the preferred cucurbitaceous plants are absent. Passing now to Eastern Asia, India, Japan, Malaya and Australia we find two general types of food preference exhibited by several species of *Epilachna* that occur in these regions. *E. vigintioctopunctata*, which extends from India through southern China into Java, the Philippines and finally into Australia, feeds generally upon potatoes, often becoming a severe pest and appearing also on other solanaceous plants. These latter include tomato, several wild or introduced species of *Solanum* as well as *Datura* and *Physalis*. In the western part of its range, however, it frequently appears on cucurbits, as we have noted is the case with the European and North American species, and once in Australia it has been found on cotton. Several other south Asiatic species likewise affect Solanaceæ. Similarly the Japanese *E. niponica* effects both Cucurbitaceæ and Solanaceæ, having been noticed particularly on the commonly grown garden vegetables belonging to this family, as well as rarely on unrelated plants such as cherry. In South America at least two species, *Epilachna clandestina* and *E. pænulata* affect various cucurbits, but no forms feeding on Solanaceæ appear to have been reported from that continent. Finally, in Africa five species, *E. dahlbomi*, *E. godarti*, *E. matronula*, *E. polymorpha* and *E. similis* have been found feeding on cotton, a malvaceous plant not related to those previously mentioned (except single recorded instances of *Epilachna* on cotton in Australia and Malaya) showing the existence of another type of food preference among the Ethiopian species of *Epilachna*. I have outlined in some detail the food preferences of *Epilachna* as they show transitions that indicate a remarkably clear correlation between distribution and food-plants.

In one other tribe of Coccinellidæ, the Veraniinæ, five species feed on Gramineæ and represent a second independent shift from predatory habits.

A further independent development of phytophagy of a specialized type is seen in another small series of Coccinellidæ where several genera have become mycophagous. This habit has been frequently observed in species of *Thea*, *Vibidia* and *Halyzia*, (Lichtenstein, '17; Martelli, '10–'14; Stroubal, '26; Tokura and Kakuta, '30), all of which belong to the tribe Psylloborini. Here the food consists gen-

erally of the spores as well as conidia and perithecia of various fungi (Perisporiales and Mucedineæ).

Some other observations indicate that vegetable material such as pollen occasionally enters into the dietary of other coccinellids or that they may very exceptionally feed to some extent on foliage (Brassler, '30), but such behavior appears to have no definite status so far as the general habits of species are concerned.

III. CHANGE FROM PHYTOPHAGOUS TO SAPROPHAGOUS HABITS

Certain Lepidoptera serve very well to illustrate modifications in food habits where plant food is replaced by dead organic matter of animal origin. This method of larval sustenance is of course painfully evident in the case of our common clothes moths and it extends to certain related forms as well as to other more widely different members of the order. Clothing is not a direct product of nature, but the materials from which it is made are but little changed during the process of manufacture, particularly in the case of woolen, fur and feather garments, so that it is to these that we must go to search for the origins of such household pests and their associates under natural conditions. The food of the caterpillars of the two common clothes moths (*Tineola biselliella* and *Tinea pellionella*) is generally confined to animal fibers: fur, wool and feathers derived from the higher vertebrates and containing keratin. Silk and vegetable fibers are quite consistently refused, although various materials may serve for at least partial development and the caterpillars have even been reported on occasion to become predatory and feed on mites (Webster, '17), or even become cannibalistic, feeding on pupæ of their own species (Illingworth, '17). A reported infestation of sugar (Dingler, '28) may perhaps involve this carnivorous habit also. The natural occurrence of related forms as epizoic parasites where they feed in the fur of mammals, is well known. A group of pyralidid moths feed as larvæ on the fur of living sloths. These belong to three related neotropical genera, *Cryptoses*, *Bradypodicola* and *Bradypophila*, extending from Central America into Brazil where they have been found on numerous occasions (Dyar, '08a, '08b, '12; Goeldi, '93; von Ihering, '14; Spuler, '06), always in this very unusual habitat. Another moth with comparable habits is *Tinea vastella*, a case-forming moth described by Busck ('10) from East Africa. In this case the larvæ burrow into the horns of antelopes where they feed on materials closely similar to those utilized by the fur-moths.

The normal food nutriment of the caterpillars of both species of clothes moths is the keratin present in the animal hairs (Sitowski, '05; Schulz, '25). It is, however, evident that many other materials (Colman, '32; Fricklinger, '20; Griswold, '33) suffice in view of the occasional predatory behavior observed, as well as the occurrence of larvæ in boxes of dried insects. Moreover, their rapid development in fish-meal and an acceleration of growth noticed on the addition of dried yeast to their food indicates quite positively that they are not limited to any specific type of food. This is further demonstrated by *Tineola uterella*, known to feed on dried fruits as well as woolen material (Kea, '33). The same is true of numerous other tineids, particularly many case-bearing forms which are scavengers. Sometimes more definite associations are formed as in the case of an œcophorid, *Neossiosynœca scatophaga* (Turner, '23) which has been found in parrots' nests in Queensland.

Another development of saprophagy

among Lepidoptera occurs in the subfamily Galleriinæ of the Pyralididæ, two members of which (*Galleria mellonella* and *Achroia grisella*) live as caterpillars in hives of the honey-bee (8). These are appropriately known as wax moths since the larvæ subsist upon the waxen comb in combination with refuse material such as larval and pupal exuviæ, excreted nitrogenous material and the like (Borchert, '33; Dickmann, '33; Kranche, '33; Kunicke, '30; Manunta, '33; Metalnikov, '08; Röber, '33; Sieber and Metalnikov, '04). Wax is an essential part of their diet. These species are thus true scavengers and their habits are firmly fixed as inquilines in the hive. Curiously enough *Achroia grisella* has been reared successfully (Götze, '29) from the seeds of a wide variety of herbs and trees, but this is by no means a normal habit.

IV. CHANGE FROM PARASITIC TO PHYTOPHAGOUS HABITS

Perhaps the case that will illustrate best the development of phytophagy in a group of ordinarily parasitic insects is a series of chalcid-flies that are plant-feeders (9). The vast majority of the forms which constitute this superfamily of Hymenoptera are entomophagous parasites affecting the eggs, larvæ or pupæ of very diverse insects in many different ways. As the group is extremely large and complex it presents great difficulties to the taxonomist, while the generally small or minute size of the individual insects makes the study of their life histories slow and arduous. Since the parasitic chalcid-flies are very important in regulating the abundance of many economically important insects and the phytophagous forms include a number of destructive pests, the habits of a large number of species have been carefully worked out until we now have a fairly accurate notion of the way in which parasitism and phytophagy appear within the group.

On account of the great preponderance of parasitic types among the existing species of Chalcidoidea, the obvious supposition is to regard the phytophagous habit as secondary or derived. An interest and slight acquaintance of the group, extending over many years, has convinced me that this has indeed been the course of evolution and that certain originally parasitic types have adopted a fixed vegetarian diet. This conclusion has been reached and very adequately defended by Gahan ('22) on the basis of a wide personal knowledge of both the taxonomy and the biology of the group. The main evidence for the validity of this view depends upon the following facts: 1) Phytophagy appears in an erratic way in at least six (excluding the entirely vegetarian fig-insects) of the fifteen or more families into which the Chalcidoidea are usually divided. 2) The phytophagous forms are always similar to the prevailing parasitic types in each family, less numerous in species and sometimes so closely related that they may not show even generic differences; in other words, the phytophagous forms show little morphological change corresponding to their habits, indicating their recent development. 3) Some species are parasitic during early life, later feeding to maturity on plants. This has been shown to be the case among certain Eurytomidæ (Rimsky-Korsakow, '14; Phillips, '17; Nielsen, '06) of the genera *Eurytoma* and *Harmolita*, both of which include also numerous entirely vegetarian species that eat seeds or produce galls on grasses. This transition in food habits is particularly important in this connection and recalls the reverse condition we have already mentioned in lycænid caterpillars where phytophagy precedes predatism during

ontogeny. 4) The dependence of phytophagous chalcid-flies upon the seeds of plants is a natural transition since these are rich in fats and proteins, approaching in composition at least roughly the food of their parasitic relatives. The extensive genus *Megastigmus* and some of its allies of the family Callimomidæ also develop in the seeds of plants, especially trees. The gall-makers appear to be, at least in some cases, related to forms that are parasites of gall insects, indicating some similarity in habitat and in the vegetable food to which their ancestors may have been accustomed, albeit in a metamorphosed condition, in the bodies of their gall-making hosts.

Why the chalcid-flies should have produced so many secondarily phytophagous forms while the other two large groups of parasitic Hymenoptera have not done so seems to find no explanation at the present time.

The larva of at least one species of Ichneumonidæa (*Grotea anguina*) is mainly phytophagous. It was found many years ago by Graenicher ('05) in the nest of a bee (*Ceratina*) where it destroys the egg or first stage larva of the host-bee and later consumes the store of bee-bread in the nest, after the fashion of a parasitic bee; it then makes its way to an adjoining *Ceratina* cell to complete its growth at the expense of a second larva. The *Grotea* larva is of course entirely vegetarian after the killing of the minute bee-egg or first larva until it later attacks the larger second larva.

V. DISCUSSION

The foregoing account of aberrant food-habits among a variety of insects shows that many such cases have several features in common, in spite of dissimilarities which are everywhere apparent. Shifts in the basic methods of feeding have occurred frequently and have not appeared, so far as can be ascertained, on any predictable basis.

The difficulty of predicting the association of parasitic insects with their hosts on the basis of natural relationships has been pointed out by Thompson and Parker (The Problem of Host Relations, with Special Reference to Entomophagous Parasites, *Parasitology*, vol. 19, pp. 1–34, 1927). These authors have not considered, however, the bearing of this on the origin of new host relations. Here the situation is not so clear since the mutual adjustments of host and parasite are much more complete than they are among the types of insects discussed in the present account.

It is true that some groups are more plastic than others in this respect and in a group where one unusual type has arisen, others are apt to be met with, as for example the generalized tineoids and specialized lycænids among Lepidoptera. Two characteristics of these changed habits indicate conditions closely similar to those associated with mutations in the structure of bodily parts. The change very frequently appears to be sudden and complete and from the nature of the case such most often needs be true where a change of habitat is involved. Even without the latter complication it is certainly not the rule to find any species indiscriminate, for example in its use of animal and plant food. Such cases do occur, *e.g.*, in the long-horned locusts mentioned earlier, but these do not appear to represent a step in the development of predatism, as a purely carnivorous diet has, so far as is known, not developed anywhere in the Orthoptera. A second characteristic feature of these shifts is their constancy when once established. They become hereditary and fixed for long periods. In the phytophagous coccinellids a sufficient time has elapsed for a whole subfamily with numerous genera and a great many species to become differentiated. Meanwhile no further shift in food-habits has occurred and the Epilachninæ retain their acquired vegetarian appetites. One may only hazard a guess as to the time involved, but from our general knowledge of Tertiary insects it certainly runs into many millions of years.

Granted that these changes have since remained so firmly fixed in the genetic constitution of a group that they show no tendency to revert to the previous condition, we may ask whether they have a physiological basis. Are they dependent upon physiological necessity, in that they represent necessary or advantageous shifts from a nutritional or purely digestive standpoint? There is some experimental evidence on this phase of the question, but unfortunately it is not so far of adequate extent and there is no promise that it may soon be greatly extended. The application of any experimental method to determine the factors which underlie the choice or selection of foods as related to their actual availability is not easy when dealing with insects. We know only that certain, often very specific foods are acceptable, sometimes only a single species of plant and that offerings of anything else are steadfastly refused, even to the point that actual starvation supervenes. However certain we may be by analogy with other species that the experimental subjects are refusing foods perfectly appropriate for assimilation, their apathy recalls the jailed fanatic on a hunger strike and further experimentation is fruitless. The use of synthetic foods as media for some species and the addition of extracted substances from peculiar foods like beeswax in connection with the wax moth have demonstrated the actual necessity of some specific substances in certain cases, but the principal experimental data relate to more general matters such as vitamin requirements and furthermore they must usually be confined to species normally accustomed to variable or mixed diets. Although the possibility of physiological adaptation cannot be excluded as a primary factor, there seems to be no evidence that changed nutritional requirements precede shifts in food-habits or even that they are coincident with them.

Neither are shifts in food-habits necessarily preceded or accompanied by essential anatomical changes in the mouthparts or other organs which are more or less intimately connected with feeding. Frequently, of course, profound structural modifications appear in predators or parasites with very specialized habits, for example those previously mentioned in lycænid caterpillars where the symphilic honey-glands or snout-like head appear among these secondarily carnivorous larvæ. As exactly similar modifications appear here and there in groups where no such shifts in habits occur, there is certainly no reason to believe that they precede rather than accompany or follow the specialized habits of their possessors. This is perhaps approaching dangerously near the oft-repeated query as to whether changes of form follow or precede changes in function, but it is clear that the present implication is quite different. Since in our present series morphological changes are not always present, they are not necessarily associated with shifts in habits, and we cannot therefore link the origin of changed habits with structural modification.

There remains the probability that many of the changes in food-habits which we have been considering are primarily due to changes in instinct which are neither dependent upon, nor correlated with changes of any other sort, either morphological or physiological. The instinctive selection of food by those insects which are definitely restricted to a limited dietary is in its perfected state infallible or practically so. The occasional instances observed where a species may lay its eggs on food which its larvæ will not accept usually result in disaster for the offspring, although we have good reason to believe that quite generally the larvæ might perfectly well grow to maturity were it not for their refusal to accept the unac-

customed food. Such aberrations are rare, but are more frequent than others where larvæ shift to strange food without any parental suggestion. We usually regard the instinctive selection of the food-plant by an ovipositing insect and the subsequent feeding of the larva on the food selected by the mother as phases of the same specific attachment to that particular plant. Certainly both actions are perfectly adapted to each other, and they must be coincident if the species is to continue in proper adjustment to its environment, but we have no assurance that they can never change independently.

Since it must be admitted that instinct is the determining factor both in selecting food plants and utilizing them, there seems to be only one conclusion that may be drawn. When the normal repetitive chain of these instincts is dislocated new food relations may appear. And further, they may persist without discontinuous subsequent modification, as hereditary aberrations of these instincts are very rare. We must attribute the origin of the types of aberrant food habits dealt with on the preceding pages to basic hereditary changes in instinct. These have originated just as they have in purely phytophagous insects where some circumscribed series becomes dependent upon food-plants widely different from those utilized by the general group to which it belongs. Many cases of this sort are well known (Brues, '20).

It is difficult to appreciate the absolute rigidity of the instincts with which we are dealing and their consequent effects in preventing so completely the development of the more diversified food-habits found in most non-parasitic animals, including many insects.

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THE PRINCIPLES OF BIOCOENOLOGY

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THE present review is the exposition of a series of recent investigations in quantitative biocoenology. Its object is to demonstrate certain principles of an experimental approach to the structure of the associations of organisms or biocoenoses. In the study of these associations in the past, investigators laid stress on the morphological side, and scarcely felt the need for applying here an experimental, analytical method. However, it would be as illogical to limit oneself to the morphological investigation of the biocoenosis as to study an aeroplane as though it were an inert and static machine. It is now beginning to be generally recognized that the biocoenosis as a dynamic unit possessing a primitive organization ought to be studied with the aid of the analytical as well as the morphological method.

If a separation of the morphological point of view from the functional one was to a certain extent justified in the past development of cytology, and *idiobiology* in general, there does not seem to be any such justification in modern biocoenology. The laws of form depend here so evidently on the dynamics that any attempt to establish the properties of a structure independently of its transformations is destined to failure. But in our usual observations under natural conditions the complexity of the environment prevents the drawing of reliable conclusions as to the causes of the transformations. Great opportunities are therefore given here to the experimental method, which can be applied *in nature* as well as in the laboratory. The technical possibilities of experimentation in biocoenology are extremely great. We can directly see how the separate components and elementary processes of the struggle for existence become organized into a whole, and how the laws of form evolve out of the laws of dynamics.

In the present review the mode of approach to the study of organization of the biocoenosis is decidedly an analytical one. At the same time we emphasize the fact that we are only concerned with the principles of organization, and that there remains a great deal of experimental work for their further concretization. The literature on the elementary processes of competition between the components of a biocoenosis has been already summarized by me in *The Struggle for Existence* (1934) and *Vérifications expérimentales de la théorie mathématique de la lutte pour la vie* (1935), and there is no need to repeat it here.

THE BIOCOENOSIS AS AN ORGANIZED UNIT

1. The recognition of the existence in nature of communities of living organisms or "biocoenoses" probably dates back to the ancient Greeks. In the modern period many botanists endeavored to understand the mutual relations among plants, and the following definition, due to Möbius (1877), is frequently quoted in hydrobiology:

> Every oyster bed is in a certain degree a community of living organisms, a combination of species and a population of individuals which find here everything needed for their growth and multiplication. As yet science has no word by which such a community of living beings might be designated, no word for a community where a total of species and individuals is mutually limited and selected under the influence of

average external conditions of life. . . . I propose the word *biocoenosis* for such a community.

The turning point in the history of biocoenology has been the publication of numerous botanical investigations at the close of the last and the beginning of the present century, which demonstrated that the vegetable covering of the earth is divided into natural units of structure or associations. The establishment of a definable unit has automatically led to greater precision of observation and of thought.

If the significance of the biocoenosis as a unit of structure in the living cover of the earth (including animals and plants) does not leave any room for doubt, the degree of organization of this unit is far from being definitely understood. Morphological observations on the structure of biocoenoses show that the latter are characterized by a definite tectological composition and by a definite "texture." In other terms they consist of definite elements in a fixed numerical relation with each other. Elton (1933) remarks, for instance, that the total number of species in an association is a fixed one, and is determined by some important principle. The limitation of the number of species (of which we will become convinced further on) is apparently connected with the limited number of the "ecological niches" which can be utilized by different species without expelling one another, as the number of species saturating the habitat is greater in a more diverse environment. Consequently a biocoenosis consists of only a part of the forms that could potentially enter into its composition. It is already organized in the sense that its membership is a limited one.

The general criterion of an "organized" system is the presence of firmly established relations maintained by regulation and we will evidently have to decide by means of some kind of dynamic method whether or not this definition holds true for the biocoenosis. *Do there exist any constant characters of constitution and of structure maintained by regulation? In other words, can certain combinations of organisms be stable ones, and the intermediates between them not, even under intermediate conditions?* The solution of this problem can be easily reached with the aid of the analytical method.

A comparison of the organization of a biocoenosis with that of living matter is sometimes made. But such a comparison is scarcely justified at the present time. First of all we have not yet any sufficiently clear understanding of the organization of living matter itself. The underlying units of its constitution are much smaller than those which are revealed by the microscope and scalpel. We can only hope that in the future we shall obtain a better insight into the laws of the molecular organization of living matter. The formation of an organized system on the primitive level of a biocoenosis ought to be therefore considered as an independent and important problem, which at the present time is quite ready for analysis.

2. Let us briefly examine certain observations in field conditions concerning the properties of the biocoenosis as a unit of structure. First of all arises the question whether there exists a sharp spatial separation of one type of structure from another. A number of botanists (Du Rietz, 1921, 1930; Chouard, 1932) give an affirmative answer to this question. In spite of the variety of conditions continuously passing from one value to another only a limited number of distinct associations can be usually established. One complex is sharply separated from another, and the intermediate combinations of species are not observed. However, no unanimity on the subject has been yet

attained (Gleason, 1926) owing to the complexity of field conditions.

To establish objectively how one kind of structure is separated from another an investigation is usually made as to transition of one type of distribution of organisms in space into another. The essential characteristic of the type of distribution in space is relatively simple. We calculate in how far the components of the biocoenosis are distributed in space at random (or not at random), and how sharply a statistical law of distribution peculiar to one association passes into another law in a new association. Regarding many components indications exist that they are not scattered in the association according to the laws of chance, but are rather grouped into aggregations (Gray and Treloar, 1933; Allee, 1934). Then the character of the statistical distribution of such mosaic complexes or aggregations in the biocoenosis can serve as a criterion of the homogeneity of the latter. If the biocoenosis is homogeneous, the aggregations for their part can be distributed in it according to the laws of chance.

A very accurate method for investigating the character of the spatial distribution of the components in the biocoenosis has been elaborated by The Svedberg (1922). We can divide a plot under investigation into N squares, count the number of individuals of a certain species found on the square (v_1) and establish the mean value or abundance (v). The statistical investigation shows that if the individuals (or components in general) are distributed according to the law of chance, the square of the standard deviation σ^2 (of the variation series constructed with the values v_1), divided by the square of abundance (v^2) and designated as the relative square mean fluctuation δ^2 must be equal to the inverse value of abundance $\frac{1}{v}$:

$$\delta^2 = \frac{\sigma^2}{v^2} = \frac{1}{v}$$

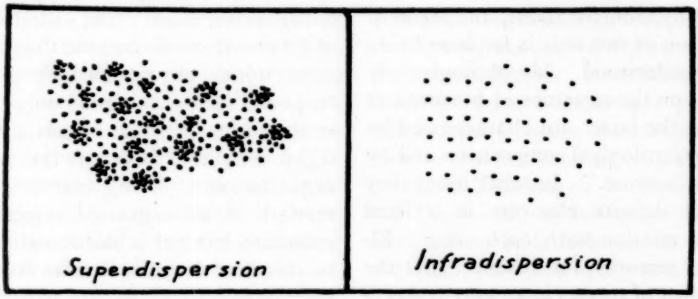

FIG. 1. TWO TYPES OF THE DISTRIBUTION OF ORGANISMS IN SPACE

Representing $\frac{\sigma^2}{v^2}$ as the δ^2 found, and $\frac{1}{v}$ as the δ^2 calculated, it can be said that if the components are distributed at random the ratio δ^2 found/δ^2 calculated must be equal to 1. This ratio is called *the coefficient of dispersion*. Every deviation from random distribution in space leads to a deviation from unity of the value of the coefficient of dispersion. Thus, for instance, if the components are distributed in aggregations the per cent of the squares bearing the number of components deviating from the mean value will be greater than we might expect from normal distribution. The δ^2 found will be greater than

$\frac{1}{v}$ and the coefficient of dispersion will be > 1 (Superdispersion, Fig. 1). But if the components are distributed too regularly (for example the stems of moss when very close together) the coefficient of dispersion will be smaller than the unit (infradispersion).

3. The most important structural property of the biocoenosis is the existence of definite quantitative relations between the abundant species and the rarer ones. In this connection let us consider biocoenological terminology. The *abundance* of a species is characterized by the number of individuals on a unit of surface, and the degree of domination by the per cent of

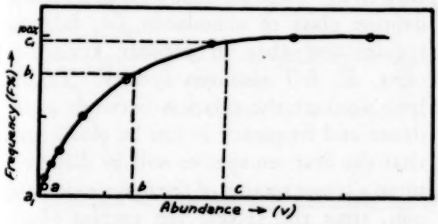

FIG. 2. THE RELATION BETWEEN ABUNDANCE AND FREQUENCY IN THE SNAIL, VALLONIA PULCHELLA
(According to Beklemishev, 1931)

abundance of a given species in the abundance of the total population. Another characteristic represents the *frequency*, or the per cent of the samples in which the individuals of the given species have been found in proportion to the entire number of the investigated samples. If we have examined a hundred samples and found a definite species in twenty-five of them the frequency will be 25 per cent. Frequency represents a complicated statistical characteristic which depends on abundance, the size of the sample and the type of the distribution of the organisms on the plot. On a plot of large size we will find all the organisms of the biocoenosis and frequency will become simply transformed into a list of the species. It is very important to bear in mind the connection between frequency and abundance with the constant size of the sample plot. This connection will depend on the character of distribution of the organisms in space. For the simplest case of a normal dispersion frequency will be an exponential function of abundance: $F\% = 100\ (1 - e^{-v})\%$, where $F\%$ is frequency and v abundance. Figure 2 represents this relation often encountered in practice (Beklemishev, 1931; McGinnies, 1934). With the increase of abundance frequency approaches gradually to 100 per cent on the typical saturation curve.

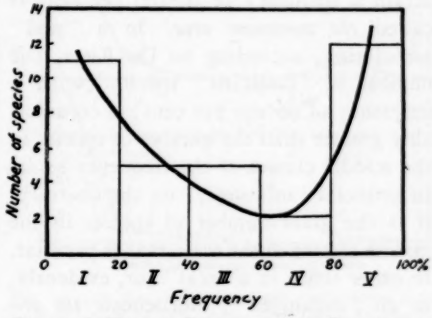

FIG. 3. A TYPICAL CURVE FOR THE DISTRIBUTION OF FREQUENCIES
(According to Du Rietz, 1921)

In spite of the great complexity of such a characteristic as frequency many authors have often used it in the investigation of the structure of associations. With a certain moderate size of the sample plot (upon which the frequency of only the most abundant species attains 100 per cent and in others is still very low) we can group frequencies into, for instance, 5 classes: 0–20, 20–40, 40–60, 60–80, 80–100 per cent and determine the number of species which belong to each of them. Jaccard (1902) was the first to build such curves, and Raunkiaer established the following law (Raunkiaer, 1918; Kenoyer,

1927; Gleason, 1929): the greatest number of species belongs to class 0–20 per cent, i.e. they are rare. As the order of the class of frequency rises the number of species belonging to it decreases and reaches a minimum in the fourth class (60–80 per cent) and then rises again in the fifth class (80–100 per cent), attaining a second maximum on the greatest frequencies (Fig. 3). In this manner it becomes possible to separate out of the whole mass of species in the biocoenosis a certain definite group of the most frequent ones which Du Rietz (1921) calls *the constants* of the association. The size of the sample plot upon which these species attain a frequency of 90–100 per cent is called *the minimum area*. In a "real" association, according to Du Rietz, the number of "constant" species (with a frequency of 90–100 per cent) is considerably greater than the number of species in the middle classes of the frequency scale. In artificial "mixtures," on the contrary, it is the great number of species in the middle classes of the scale that is peculiar. In other terms in a "real" (or, evidently, in an "organized") biocoenosis *the predominating part of the biomass belongs to a separated group of frequent or constant species*. This is due to the fact that the organized association is the product of a long process of struggle for existence and of mutual aid. Here survived a few species or combinations of species that are more successfully adapted to particular ecological niches of the habitat and they constitute the basic biomass of the association. There is evidently no such structure in an unorganized mixture. Thus, according to Du Rietz, we can consider the structure of the association as the outcome of a long process of competition and selection.

4. We will soon see that the presence of a definite structure in the biocoenosis may or may not correspond to a state of organization. One can judge of this latter only by the dynamic and not by the morphological properties. But let us now consider certain difficulties in the work with frequencies. It has been repeatedly pointed out (Gleason, 1929; Romell, 1930) that frequency represents a complicated statistical characteristic, and that in this connection the causes of an accumulation of species in the maximal (fifth) class of frequency require a special analysis. *Does this accumulation reflect the very essence in the structure of the biocoenosis—a certain natural separation of a group of constant species—or is it a statistical artifact?* The possibility of the latter has been mentioned by Gleason (1929). Let us now turn to fig. 2 and suppose that in a certain definite class of abundance, *ab*, fall ten species and that in another analogous class, *bc*, fall also ten species. Taking into account the relation between abundance and frequency it can be easily seen that the first ten species will be dispersed upon a larger section of the frequency scale, a_1b_1, than the second ten species (b_1c_1). In this manner, owing to the exponential relation between abundance and frequency, the most numerous species widely distributed on the scale of abundance can become artificially grouped on a very small section of the scale of frequency. The considerations advanced by Romell (1930) lead also to a notion of the great statistical inclusiveness of the last class of frequency, although his arguments are of a somewhat artificial nature. If we add to this the influence upon frequency of the size of the sample plot and of the character of the dispersion of the organisms in space we will easily come to the following conclusion: *for obtaining an objective representation of the structure of the biocoenosis we must have recourse to some characteristic simpler than frequency*.

The most convenient for this purpose is

the abundance of organisms. In fact it often turns out that the constant species are at the same time the dominant ones, i.e. they predominate as regards abundance (Katz, 1930). Du Rietz (1930) directly introduces the existence of constant dominants in every layer of vegetation into the definition of a phytocoenosis. It is therefore interesting to examine upon existing facts to what extent the group of the most abundant or dominant species is naturally separated in the structure of a biocoenosis. We can analyze the relation between the class of abundance and the number of species belonging to this class. It is often supposed (Gleason, 1929; Beklemishev, 1931) that this relation is of a simple statistical character. In other words the greater the class of abundance the less numerous is the number of species belonging to this class, and in this way no natural separation of a group of abundant species can be observed. However, it is not difficult to see that the situation frequently differs. In Figure 4 are given the curves we have constructed on the basis of the data of Beklemishev and his collaborators (1931). The curve (1) shows the distribution of 26 species of forest mites in the classes of abundance in the lichen stratum of *Pinetum*-association, and curve (2) that of 23 species of plants in the association of *Filipenduletum*. In both cases the sharp separation of two types of species—the abundant and the rarer ones—is quite apparent. The total population is sharply divided into two categories: the numerically dominant species and the non-dominant ones, represented by a small number of individuals. Consequently we arrive here at a conclusion corresponding to that of Du Rietz—the basic biomass of the biocoenosis belongs to a few dominant species. (For such calculations abundance ought to be expressed in biomass, and not in the number of individuals.)

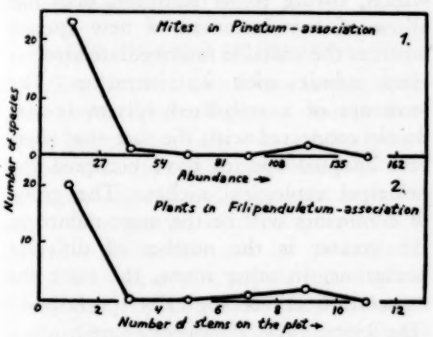

FIG. 4. THE RELATION BETWEEN ABUNDANCE AND THE NUMBER OF SPECIES

(1) Distribution of 26 species of mites. Data from Beklemishev, 1931. (2) Distribution of 23 plants. Data from Beklemishev and Igoshina, 1928.

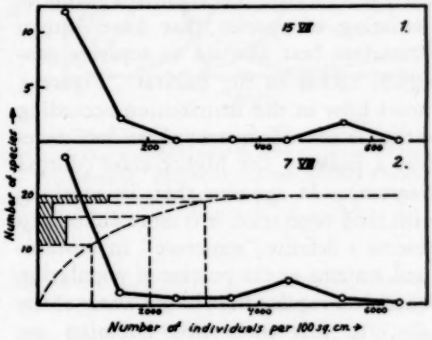

FIG. 5. THE RELATION BETWEEN ABUNDANCE AND FREQUENCY IN THE POPULATING GLASS PLATES SUBMERGED IN THE WATER

(1) young and (2) mature biocoenoses. Data from Duplakov, 1933

5. An interesting example from hydrobiology shows that a specific structure can exist in organized as well as in unorganized biocoenosis. Thus Duplakov (1933) following the method of Hentschel (1916) investigated the process of population of glass plates plunged in summer into the water in the shore zone of a lake in Middle Russia. Three days after the beginning of the experiment (15.VII) there was on the glass a typical immature and unstable biocoenosis in which the group of

dominant species was at the same time sharply apparent. On the basis of his data we constructed the curves given in Figure 5. The dominants of the immature biocoenosis were simply the species abundantly represented in the surrounding medium, fixing upon the glass and growing rapidly. Such a feature of an organized state as the regulation of the composition was here entirely lacking. The biocoenosis changed rapidly and only later become somewhat stabilized as regards its qualitative composition. In such a mature biocoenosis (7.VIII) one can also distinguish a group of dominants, but now consisting of species that have shown themselves best adapted to separate ecological niches in the habitat. Figure 5 shows how in the distribution according to the classes of frequency these dominants give a peak in the higher class (dotted diagram). It appears that in working with land vegetation it is more difficult to observe a definite "structure" in unstabilized systems as the process of population is here less regular than in the water of the lake. In this connection botanists use another structural method for recognition of the stabilized biocoenosis (Chouard, 1932). Peculiar to the latter is the presence of a sharply outlined type in the number of species per unit of surface: the variability in the number of species in the sample is represented by the normal variation curve. In the case of unstabilized biocoenoses owing to the irregularity of dispersion there is no sharply outlined typical number of species holding good for the entire territory. The variation curve of the number of species in the sample is irregular and shows several peaks. But in the case of a glass plate being populated in the lake the course of the population is so regular that an immature biocoenosis also possesses a "type." In this way the existence of a definite structure shows often, ***but not always***, a stabilized state of the system. The necessity of a combined morphological (structure) and dynamic (stability) approach to the understanding of organization of biocoenoses is obvious, and it is already recognized by botanists (Du Rietz, 1930).

6. Turning to the structure of stabilized systems we must point out the important principle elaborated by Clements (1916) concerning the very process of stabilization. His observations on vegetation led him to the idea of a gradual development of a stable type of association or *climax* which, owing to its stability, does not allow of any intrusion of new species whereas the unstable intermediate associations admit such an intrusion. The structure of a stabilized system is evidently connected with the fact that some best adapted species have occupied the principal ecological niches. The group of dominants will be the more numerous the greater is the number of different niches or, in other terms, the more the association is "ecologically specialized" (Du Rietz, 1921; Lundbeck, 1926). In a more homogeneous environment the number of dominants falls (Frey, 1927). In any case we can say with certainty that at the basis of the structure of a biocoenosis lies the "niche" structure. The group of rare species is apparently a heterogeneous one and includes the immigrants coming from neighboring habitats, and those individuals that find convenient conditions for living on the various plots existing together with and between the basic niches. The fact of the group of abundant species being usually separated from that of the rarer ones represents a proof of the absence of a continuous transition between the dimensions of the fundamental niches and those of the additional plots. This regularity is especially apparent in the separate layers or *sinusia* of the biocoe-

nosis (Du Rietz, 1930), as the structural properties are here not so much overshadowed by the statistical variability of dimensions of the basic niches.

Summarizing, it can be remarked that the biocoenosis possesses a definite structure whose degree of organization must be investigated experimentally. Field observations raise before us the following problem: How under continuous change of the environment from one value to another can arise stable, spatially separated structures whose composition is maintained by regulation? In other words, how does a state of organization arise?

ON THE PRINCIPLES OF ORGANIZATION

1. The simplest way of answering these questions will be to begin an examination of the principles of organization by pointing out that there exist biocoenoses of two types: the *unstable* and the mature or *stable* ones. The process of development leading to stabilization can be particularly well observed on the population of glass plates plunged in natural fresh waters. Recent observations (Ivlev, 1933) show that the process of development of such a biocoenosis falls pretty regularly into two periods: a period of *accumulation* with a simultaneous growth of all the principal components of the biocoenosis, and a later period of reconstruction, when under the influence of competition and of other biocoenotic relations a part of the components is suppressed and begins to diminish in number whilst others develop in even greater abundance (Fig. 6). However, in fresh waters of our latitude a final stabilization of the system is never attained. Having reached a certain stability it continues uninterrupted alteration under the influence of variation of the external medium and finally dies off almost completely in the winter period. It is therefore easy to understand why the idea of "moving equilibrium" is particularly wide-spread among hydrobiologists (Resvoy, 1924).

Recently Duplakov (1933), whom we have already mentioned, carried out a very careful investigation of the process of population of glass plates submerged in Lake Glubokoe (near Moscow), and we

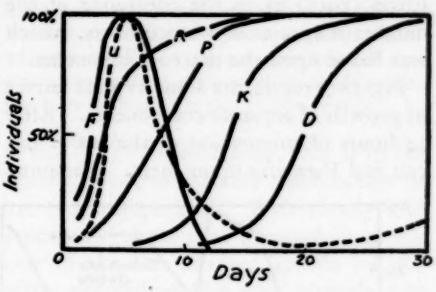

FIG. 6. THE DEVELOPMENT OF POPULATION ON THE GLASS PLATE SUBMERGED IN THE MOSCOW RIVER
F-non-motile *Flagellata*, *U*-non-motile *Protozoa*, *R*-moving *Rotatoria*, *P*-moving *Protozoa*, K-non-motile *Rotatoria*, *D-Diatomaceae*. From Ivlev, 1933.

TABLE 1

The increase of the number of species in a biocoenosis. (Glass plate submerged in Lake Glubokoe.) According to Duplakov, 1933

DAYS AFTER BEGINNING OF THE EXPERIMENT	NUMBER OF SPECIES
1	13*
3	20
5	33
7	33
9	43
26	47
42	45

* Five of these will disappear on the ninth day.

will discuss here some of the results obtained. Table 1 shows that the number of species in the populating biocoenosis continuously increases after the submersion of the glass plate into the water and attains a certain stability towards the ninth day (43 species). This number remains approximately constant up to the forty-second day. The slight alterations

occur only at the expense of accidental immigrants represented by an insignificant number of individuals. Some of the first settlers soon disappear, but from the ninth to the forty-second day the qualitative composition of the biocoenosis remains almost the same. These data are therefore in accord with the view of Elton (1933) as to the constancy of the number of species in a biocoenosis, which was based upon the macro-components.

Figure 7 represents some typical curves of growth of separate components. After 24 hours of submersion of the plates one can find *Vorticella* upon them. The number of these increases very rapidly and reaches a maximum after 12 days. After this the number of *Vorticella* decreases considerably under the influence of the developing filamentous algae (*Oedogonium* and *Spirogyra*), whose growth is intense in the light (whilst in the dark they are incapable of disturbing the animal nature of the biocoenosis). The expulsion of *Vorticella* from the biocoenosis by the filamentous algae can be explained by the fact that an abundant development of the latter prevents the nutrition of *Vorticella*. Indeed, by its mode of nutrition *Vorticella* belongs to the "sedimentators," and requires for the absorption of the suspended nutritive particles a free circulation of the water which surrounds them. The developing flakes of green algae interfere with this circulation. Towards autumn the filamentous algae finishing their cycle die off, and *Vorticella* develops again.

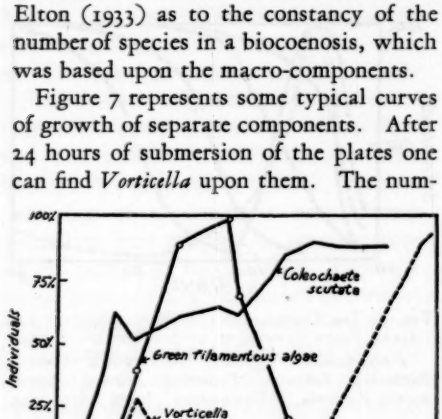

FIG. 7. SOME TYPICAL CURVES OF GROWTH OF SEPARATE COMPONENTS ON THE GLASS PLATE SUBMERGED IN THE WATER
From Duplakov, 1933

The curves of development of the lamellate green algae (*Coleochaete* and *Stigeoclonium*) are of peculiar interest. In Figure 7 is traced the curve of growth of a number of individuals of *Coleochaete scutata*. Soon after the beginning of the experiment numerous germinating algae settle down on the glass plate and begin to develop into small lamellae. Later the increase of the number of the lamellae ceases owing to a lack of room. The larger lamellae push off or cover over the young growing algae which have settled on the glass. The overgrowth of the glass by the filamentous algae is also an obstacle to their development. However, at the moment of the strong dying off of the filamentous algae and of another species—*Coleochaete soluta*—owing to seasonal causes, the species *Coleochaete scutata* increases very rapidly, taking possession of the liberated places, and later remains at a new fixed level.

It can be said with perfect assurance that the biocoenosis is subject to regular development and attains a certain state of stability which, however, is very strongly altered by the seasonal variation in the lake. The main factors of development are the biocoenotic relations between organisms—competition, destruction and mutual aid—, and if there were no seasonal changes these would be the only factors of development. The type of the external medium defines the relative advantage of some components over others and, consequently, the type of development itself, but this type is realized only by means of the biocoenotic forces (in the case of constant external

conditions). In the associations of large terrestrial plants the rôle of seasonal variations is not so profound, and it is therefore possible to observe distinctly the stability of the final states or climaxes (Phillips, 1934). The possession of organization and of regulations is usually connected only with these final states and these categories consequently represent an outcome of the process of regular development.

2. If the organization is the outcome of development we must evidently establish the factors governing the dynamics of development and express them in the form of differential equations. The solutions of these equations will indicate the stationary states and furnish complete information about the regulation of these states. The experiments made under constant laboratory conditions can easily verify the theoretical conclusions. We can also analyze the influence of the external factors on the stationary states of the system. To what extent do the properties of the system fail to change in proportion to external alterations or, in other words, why are intermediate combinations of organisms impossible under intermediate conditions? How far do the properties of the system change in an abrupt manner with the threshold values of external factors, etc.?

For the details of these calculations the reader is referred to the two books by Gause (1934, 1935) and the paper by Gause and Witt (1935); we will only briefly examine here some of the fundamental principles. The dynamics of development of a biocoenosis resulting from interaction between species can lead, for example in the simplest case of two components, either (1) to a complete expulsion of one component by the other,

In addition to the experiments mentioned by Gause (1934) interesting data on the instability of microbic associations in the same ecological niche and on the consequent expulsion of some components by others may be found in Nicol (1934). He writes: "M. Beijerinck's view of the condition of associations of bacteria responsible for the production of commercial preparations of soured milk may be expressed by saying that these associations are in unstable equilibrium. On account of this instability it is not possible to continue inoculation of fresh milk from a properly soured sample indefinitely; after a very few transfers the balance has been so much disturbed that an undesirable product results from fermentation. Commercial quantities of yoghurt are therefore made from continually renewed mixtures of the single species, which are maintained in pure cultures in milk."

or else (2) to a *stabilization*, that is to the establishment of a stable combination of the two components. Both theory and experiment show that a complete expulsion of the less adapted species by the better adapted one can only take place in the case of two species belonging to the same ecological niche in the habitat. The stabilization which interests us more immediately can take place in the case of each of the species possessing an advantage in its own ecological niche (a "two-niches" stabilization) or in the case of a mutual (or a one-sided) help between the species (symbiotic stabilization). If we write a theoretical equation of the interaction between the species in such a case we will come to the following conclusion. The process of interaction between the first species (N_1) and the second (N_2) will lead to a stable mixed population which will be dynamically maintained. This can be easily seen on the graph with N_1 plotted on the abscissae and N_2 on the ordinates (Fig. 8). This stable population (A) will represent a "knot" as the mathematicians call it. In other words all the curves of the interaction between species will meet in this point. If we begin with small concentrations of both species (a) they will increase until reaching "stable" values (A). If we now destroy the equilibrium artificially by

introducing more N_2 than necessary and less N_1 than is necessary for equilibrium (a_1), the "stable" combination (A) will be automatically recovered. In this manner the mathematical theory shows quite clearly *how the regulation of a type (or of a stable combination) can result from the interaction between species*.

Theoretical considerations of this kind are to a certain extent confirmed by the experimental work. The stable combination of species and its regulation can be observed in a mixed population of two infusoria one of which, *Paramecium aurelia* (N_2), utilizes more actively the bacterial

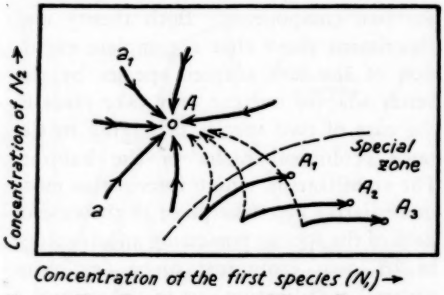

FIG. 8. THE BEHAVIOR OF A MIXED POPULATION OF TWO SPECIES BELONGING TO DIFFERENT ECOLOGICAL NICHES

The dotted lines show the direction of the curves of interaction in the absence of a "special zone."

components of the mixed diet suspended in the upper layer of the liquid, whilst the other, *Paramecium bursaria* (N_1) utilizes more actively the yeast settling on the bottom, although both infusoria can live in the entire territory of the microcosm (Gause, 1935). At the same time experimental work points to a certain limitation in the regulation of the typical combination of two species. This regulation is not possible from *all* the points on the surface N_1, N_2. If we bring the population into a "special zone" (Fig. 8) where a new factor not taken into account before is in operation (a peculiar sensitivity of N_2 to the metabolic products of N_1 and N_2), the "stable" combination (A) cannot become reestablished and we will obtain A_1, A_2, A_3, etc. It is easy to show what are here the alterations in the equation of the interaction between species (Gause and Witt, 1935). Observations of this kind are well known to ecologists. In the population of glass plates, for instance, it may be observed that certain forms enter into a "young biocoenosis" and occupy in it a corresponding place (N_2 enters readily when N_1 is not numerous), but can scarcely enter into an "older biocoenosis" (a great deal of N_1), as Karsinkin (1936, in press) remarks. This can also be compared to the facts of an incomplete regeneration of climaxes in the plant associations (Ilinsky and Pozelsky, 1929). Usually certain species cannot regain possession of the places that they occupied before.

3. We can conclude that the first feature of an organized biocoenosis—the regulation (within certain limits) of a stable combination of species—can be successfully observed in an experimental way and accounted for theoretically with the aid of a differential equation. The meaning of a regulation in the case of two species belonging to different ecological niches consists in their expelling one another into the zones of maximal effectiveness, so that every disturbance of such a stationary state leads automatically, owing to competition, to the reestablishment of the stable proportion. Such a regulation can take place also in the case of a symbiosis, when with definite relations between the concentrations of the species the greatest advantage for them is attained (see Gause and Witt, 1935). Let us now consider the second feature of the biocoenosis as an organized unit. Many authors have pointed to the fact that with an uninterrupted change of external factors the types of stable combinations of organ-

isms pass abruptly from one to another or, in other words, that the intermediate combinations of organisms are impossible under intermediate conditions. It seems that this important principle can also be theoretically and experimentally demonstrated with simple biocoenosis.

The idea of a theoretical demonstration represents an application of the mathematical conceptions of Poincaré concerning the *change of stability* in a system. If we assume that a definite biological system is under the influence of the temperature gradient which modifies the relations between the fitness of the species, the calculation will show that at fixed moments the system will undergo *qualitative* changes. One type of stable combination will be succeeded by another type of stable combination. The technical details of such calculations can be found in Gause and Witt (1935). Here we can only note that the changes in question are the result of purely biocoenotic causes: after a certain threshold some components cannot withstand the competition but at the same time continue to exist as pure populations. However, under complex natural environment we have to take into account two factors participating in formation of types: (1) biocoenotic, and (2) physiological factors, i.e. the falling out of components in passing their physiological thresholds which takes place both in pure and in mixed populations. These two groups of factors are often closely interwoven and we will now analyze them on a concrete example.

4. Let us consider briefly the results of several new experiments of the author with artificial biocoenoses of Protozoa in order to illustrate the possibilities of the experimental method here. In these experiments a study was made of the influence of a gradual change in a factor of the external medium (hydrogen ion concentration, *pH*) on the formation of the biocoenoses. An attempt was made to answer the two following questions: (1) What are the differences in structure between the unstabilized and the stabilized biocoenoses?, and (2) How sharp is the separation of one type of biocoenosis from another under such conditions?

The experiments were made in tubes for centrifugation with 5 c.c. of the liquid of the following composition: To one liter of twice distilled water add 40 mg. CaO (in boiling water), pass through CO_2 until dissolved, and then add $MgSO_4$ (5%)—0.5 c.c., $Ca(NO_3)_2$ (1%)—0.5 c.c., K_2HPO_4 (1%)—0.5 c.c., and $FeSO_4$—2 mg. to one liter. This medium is favorable to the majority of the Protozoa and its *pH*

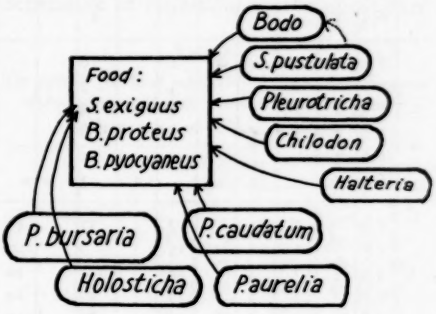

FIG. 9. THE FOOD-CHAIN IN THE EXPERIMENTAL BIOCOENOSIS OF PROTOZOA

is close to 7.9. For a gradual acidulation was used m/20 KH_2PO_4 and the following *pH*'s were established in separate cultures: 7.6; 7.3; 7.0; 6.6; 6.3. The experiments were made in a thermostat at 24.5°C. with an artificial light according to Hartmann (300 watt). Every day a centrifugation and a change of the medium were made, and likewise the number of individuals in 0.5 c.c. was counted. After the counting the protista were put back into the culture and thus there was no rarefication of the population. The food consisted of three species of microörganisms which were taken off a solid medium by means of a platinum loop and shaken up in the salt solution. To 30 c.c. was added one loop of *Saccharomyces exiguus*, half-loop of *Bacillus proteus* and half-loop of *B. pyocyaneus*.

Figure 9 shows the food-chain of our biocoenosis consisting of nine species of

TABLE 2

Growth of the number of individuals in experimental biocoenoses under different pH of the medium

(Number in 5 cc.)

DAYS	pH	*Paramecium caudatum* 0.5 c.c.	*P. aurelia* 0.5 c.c.	*P. bursaria* 0.5 c.c.	*Stylonychia pustulata* 0.5 c.c.	*Plagiotricha grandis* 0.5 c.c.	*Holosticha sp.* 0.5 c.c.	*Halteria grandinella* 0.5 c.c.	*Chilodon cucullulus* 0.01 c.c.	*Bodo sp.* 0.01 c.c.
	7.9	6	6	6	5	3	2	3	3	10
	7.6	6	6	6	5	3	2	3	3	10
0	7.3	6	6	6	5	3	2	3	3	10
	7.0	6	6	6	5	3	2	3	3	10
	6.6	6	6	6	5	3	2	3	3	10
	6.3	6	6	6	5	3	2	3	3	10
	7.9	1				2	1	1		
	7.6	4	3		1			2		
1	7.3	1	1							
	7.0		1	1	1		1	1		
	6.6	1	4		1			1		
	6.3	3						2		
	7.9	1	1	1	1	1		10		
	7.6	1	1			3	1	7		
2	7.3	2	2			2		6		
	7.0	1	5	1		6		8		
	6.6	3				4		12		
	6.3	1	5	2			1	3		
	7.9		3			7		37		47
	7.6	1	2	2	1	15		7		120
4	7.3	3	1	1		14		21		40
	7.0	1	3	5		15		40		24
	6.6	1	5	7		10		68		40
	6.3	7	2	14		2		24		62
	7.9		4	1	1	9	5	50		22
	7.6	1	2	2		22		30		12
6	7.3	2	6	8	1	24		34		16
	7.0	1	9	11	2	15		46		12
	6.6	1	4	13	2	6		80		10
	6.3	1	10	16	2	4		24		8
	7.9	1	6	3		22	5	100		24
	7.6	2	2	8		26		55	0.5	22
7	7.3	1	4	16	1	24		90		8
	7.0	1	7	10	1	9		60		5
	6.6	2	5	8	3	11		95		5
	6.3	4	9	19	4	3		40		6
	7.9		2	1		9	11	240		26
	7.6			14	1	30		230		44
8	7.3	2	3	25	6	8		140		16
	7.0		3	10	1	10		120		6
	6.6	3	7	11	3	7		150		30
	6.3	1	8	24	4	2		90		10

DAYS	pH	*Paramecium caudatum* 0.5 c.c.	*P. aurelia* 0.5 c.c.	*P. bursaria* 0.5 c.c.	*Stylonychia pustulata* 0.5 c.c.	*Plagiotricha grandis* 0.5 c.c.	*Holosticha sp.* 0.5 c.c.	*Halteria grandinella* 0.5 c.c.	*Chilodon cucullulus* 0.01 c.c.	*Bodo sp.* 0.01 c.c.
	7.9		6	5		4	36	290		10
	7.6		3	15	1	24		140		60
9	7.3		5	19	4	8		140		40
	7.0		20	8	2	11		140	0.5	5
	6.6	1	7	10	1	8		180	1	7
	6.3	3	14	27	4	5		80		60
	7.9		8	4	4	3	88	230		22
	7.6		3	31	1	20		240	1	3
10	7.3	1	9	38	7	10		300		4
	7.0		10	32	1	8		144	1	8
	6.6	1	5	26	1	8		240		8
	6.3	2	10	30	3	3		60		11
	7.9		10	1	2	6	88	300		6
	7.6	3	8	36	1	10		320		6
12	7.3	2	8	40	3	8		230		4
	7.0	1	7	40	3	4		140	1	3
	6.6	1	12	37	7	7		230		9
	6.3	3	16	47	6	5		44		12
	7.9		8	4	13		120	370	1	4
	7.6	1	4	70	3	8		120		3
14	7.3		12	58	3	6		110		3
	7.0	3	10	37	2	12		120	1	4
	6.6	1	6	37	2	16		125		18
	6.3	2	14	52	12	4		44		8
	7.9		5	1	8	4	240	350	1	8
	7.6		3	58	5	8		80		4
15	7.3		16	70	4	8		100		6
	7.0	2	3	70	2	4		110		8
	6.6		8	62	3	10		100		16
	6.3	3	12	66	4			88		5
	7.9		2	2	8	8	220	260		9
	7.6		10	80	3	13		60		5
16	7.3		13	68	5	8		88		6
	7.0		4	75	2	14		84		12
	6.6		8	70	3	10		105		12
	6.3	2	12	90	5	4		102		6

Protozoa. As a prototype for this biocoenosis was taken an association really existing in nature. It was merely somewhat simplified by a reduction of the number of components, and an important new condition was introduced: the nutritive and physico-chemical properties of the microcosm were maintained at a fixed level. The mean absolute results of the experiments are presented in Table 2, which shows the growth in the number of individuals under different conditions.

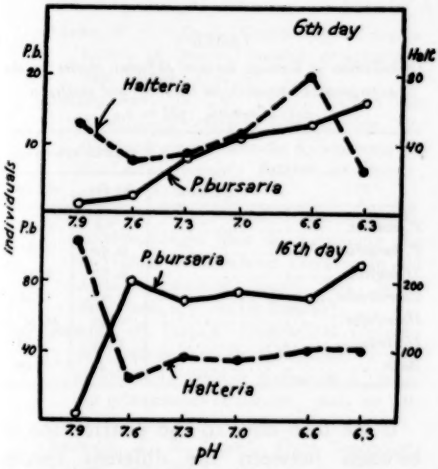

FIG. 10. THE RELATION OF SPECIES TO pH OF THE MEDIUM IN A YOUNG (SIXTH DAY) AND AN OLD (SIXTEENTH DAY) BIOCOENOSIS

An examination of Table 2 enables us to conclude that in a young immature biocoenoses (fourth and sixth days) there is no sharp separation into individualized types at different *pH*, and the differences between the types are continuous. This is illustrated by Figure 10 which shows that on the sixth day the densities of *P. bursaria* and of *Halteria* do not form any distinct types on the *pH* scale, and that no sharp differences exist between "phosphateless" and "phosphate" cultures. An entirely different picture is to be seen in mature biocoenoses (sixteenth day). They are separated into two sharply individualized types—the phosphateless (*pH* = 7.9) and the phosphate ones. A very strong increase in the concentration of the latter scarcely alters the type of the biocoenosis. Thus we have evidence of the formation of individualized units resulting from the process of development.

Turning to a more detailed analysis of the results we must point out that KH_2PO_4 together with a change of *pH* exhibits an additional specific effect on the protozoa (Beers, 1933 and Gause, 1934). In our experiments there took place a strong depression of *Holosticha* by the phosphate

TABLE 3

The separate growth of population of Paramecium bursaria under different pH of the medium. Number of individuals in 0.5 cc. Food: S. exiguus

DAYS	pH					
	7.9	7.6	7.3	7.0	6.6	6.3
2	9.5	8	8	9	10	11
4	19.5	14	13	17	18	24
5	41	35	46	54	41	40
6	67	58	44	60	50	51
7	86	70	80	70	61	86

(through not an immediate distruction, as *Holosticha* has been registered on the second day of growth). This depression is already quite distinct in the immature biocoenosis, and is therefore of a physiological and not of a biocoenotic nature. With the further development of the biocoenosis the place of *Holosticha* is taken by *P. bursaria*, which later begins to crowd out *Halteria* and is responsible for a sharp leap in the changes of concentration of the latter as regards *pH*, which did not exist before. We can say with certainty that the insufficient development of *P. bursaria* in a phosphateless biocoenosis (*pH* = 7.9) is due to the presence of *Holosticha* for, when growing separately,

P. bursaria develops in almost the same way in a phosphateless and in a phosphate medium (Table 3). In this way *Holosticha* falls out owing to physiological causes and lets *P. bursaria* into the biocoenosis on one side of the ecological scale, while on another section *P. bursaria* is pushed out (or, more exactly, not admitted) biocoenotically by *Holosticha*. The differences between the types of biocoenoses appear as a result of a complicated interweaving of biocoenotic and of physiological causes, and the stable types themselves change abruptly.

TABLE 4

Calculations of the volumes of species

SPECIES	LENGTH IN DIVISIONS OF THE OCULAR-MICROMETER	VOLUME (*P. caudatum* = 1)
1. *Paramecium caudatum*		1
2. *P. aurelia*		0.396
3. *P. bursaria*	39.9	0.405
4. *Halteria grandinella*	9.8	0.036
5. *Pleurotricha grandis*	32	0.101
6. *Chilodon cucullulus*	14.5	0.016
7. *Bodo*	2.25	0.00043
8. *Stylonychia pustulata*	63.6	0.770
9. *Holosticha*	30.3	0.098

In order to obtain an idea on distribution of the biomass between the separate species at different stages of growth of the biocoenosis we measured the species under the microscope and calculated their volumes (Table 4). These data have only the character of a very first approximation to the biomasses, as with differences of shape in the species a calculation of their volumes cannot be a very exact one. With the aid of these coefficients we can see that the surplus of biomass of *P. bursaria* in the biocoenosis with $pH = 7.6$ as compared to $pH = 7.9$ coincides almost completely with the deficiency in the biomass of *Holosticha* and *Halteria*. If we take the mean data for the fifteenth and sixteenth day we obtain: (1) an excess of *P. bursaria*: $67.5 \times 0.405 = 27.3$ and (2) a deficiency of *Holosticha* and *Halteria*: $230 \times 0.098 + 235 \times 0.036 = 30.95$. Therefore from the view-point of biomass these components mutually replace one another. An exact coincidence is hardly to be expected here owing to the approximate calculation of the volumes and the differences in productivity of formation of the biomass by different species at the expense of the same food material (Gause, 1934).

TABLE 5

Distribution of biomass between different species in the experimental biocoenosis on the sixth and sixteenth days of growth. $pH = 7.9$

SPECIES	VOLUME PER 0.5 CC.	
	6th day	16th day
P. aurelia	1.58	0.79
P. bursaria	0.40	0.81
Stylonychia	0.77	*6.16*
Pleurotricha	0.91	0.81
Holosticha	0.49	*21.55*
Halteria	1.80	*9.37*
Bodo	0.47	0.19

If we turn now to the distribution of biomass between the different species (Table 5) we will be able to note a certain difference between the immature and mature biocoenoses. In a young biocoenosis (sixth day) there are, as biocoenologists say, no "constants" in the association, that is no natural separation of the group of abundant species from the rarer ones. But such a separation appears on the sixteenth day when we have a group of rare species (0.79; 0.81; 0.81; 0.19) and of abundant species occupying the fundamental ecological niches (6.16; 21.55; 9.37). Therefore one can succeed in observing under experimental conditions the appearance of the structural properties of the biocoenosis which are usually men-

tioned in field observations. We can only remark that such a structural property is not always proof of the maturity and stability of the system. We have already had an occasion to point out that in the population of glass plates in the lake there is a very abundant fixation (and growth) of the components which will not be able afterwards to survive in the competition, and thus a structure may arise even in an immature system.

We can endeavor to summarize briefly our review by pointing out that the fundamental problems raised by field investigations—the regulation of a stable combination of species and the separation of the biocoenoses into individualized natural constructive unities or types in spite of an uninterrupted change in the external conditions—can be successfully analyzed with the aid of the experimental method. The great potentialities of this method for the future of biocoenology admit of no doubt.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

A NOTABLE CONTRIBUTION TO ENTOMOLOGY

Being a review of *A Cluster of Bees* by Tarlton Rayment, Sydney (The Endeavor Press), 1935. 752 pp., 66 plates, 100 text-figures.

By *William Morton Wheeler, Harvard University*.

Those who believe that the sturdy breed of naturalists is all but extinct and is being supplanted by academic biologists need to revise their opinion by reading the impressive volume on the bees of Australia by Tarlton Rayment, the most recent and the most catholic of the long series of naturalists who have devoted themselves to a study of the Hymenoptera, from prose-poets like Maeterlinck, Everard, Tickner Edwards and behaviorists and ecologists like Réaumur, the Hubers, Fabre, Ferton, von Buttel-Reepen, the Peckhams, the Raus, Hoffer, W. Wagner, Lie-Pettersen, Sladen, Plath, Frison, F. X. Williams, Hingston, Adlerz, Nielsen, Maidl and Grandi to taxonomists like Forel, Emery, Friese and Bequaert. To compare Rayment with any of the living members of this galaxy would be invidious, but a comparison is permissible with Fabre, of whom he says: "I admire the genius of the man; his charming poetry; his devotion to truth; his engaging simplicity; I am pleased to call him 'master'." But while Fabre has always been justly admired as an extraordinary observer and stylist, he suffered from four regrettable infirmities, which have diminished the importance of his works in the eyes of present day entomologists: he rejected evolution; his conception of insect behavior was essentially medieval and scholastic; he despised taxonomy; he was a constitutional recluse and introvert, and therefore unable to adopt the social and co-operative rôle of the true scientist. Rayment's attitude towards his subject and his fellows is so different that it merits special comment. Though primarily interested in the behavior of the solitary and social bees, he rightly treats morphology and taxonomy as the basis and framework of his investigations. His views on evolution, insect "intelligence" and the importance of cooperation among scientists may be gleaned from the following quotations chosen at random (pp. 253, 189, 164):

> "This outcropping here and there of certain specific anatomical developments, as though to demonstrate their common origin, has a parallel in the behavior of the creatures. Evolution is silently directing all life; not only the physical features, but also the mental qualities, are slowly but constantly changing. To deny the discernment of the lower animals, and to assert that bees are only 'reflex machines' is utterly unscientific, for such a contention endeavors to limit the processes of evolution to mere morphological structure and entirely overlooks the fact that brain functions, but that functioning has limits imposed by the evolutionary level already attained."
>
> "In some cases I prefer the thin, sharp point of Wheeler's thrust to the heavy broad-axe of the august Fabre— "It is with this gibberish about continuous flashes of reason that men pretend to build up science today!" Ah, master, I regret that blow!
>
> "Every day I see flashes of reason light up the eyes of my retriever dog. Why, as I write, my fire burns low.
>
> "Brown!" I call sharply; he comes in from the kitchen, stretching himself lazily.
>
> "Bring in some wood!"

He lifts his long ears a little, and cocks his head to one side; his eyes speak as clearly as our own. His whole countenance suggests inquiry.

"A piece of wood!" He did not hear aright. I repeat the command in imperative tone.

"His face relaxes, he wags his feathered tail sharply and departs on the errand.—A minute or two later he returns with a heavy mallee-root, that being the fuel I prefer for winter burning. Moreover, he is proud of his comprehension and ability to carry out the task to which he has been assigned.

"Do I believe animals have intelligence?"

To which I reply: "Nature, having once evolved a muscle, a bone, or a sinew for a certain function, never duplicates the organ. The horse, the sheep, the dog and man each have a femur-bone to enable them to walk and run, and the horse, the dog, the bee and man each have a brain to direct the essential activities of their lives. True, some animals have longer femora, and so run quicker; other animals have better developed brains, and so think more lucidly. I will not waste your time or mine on those who endeavor to prove that the thigh-bone of the apes is for a different purpose to the thigh-bone of the genus *Homo*, and that the brain of the bee has a different function to that of man."

"One of the most charming aspects of science is the universality of the brotherhood. I have only to request the authorities of the Smithsonian Institute, United States, to let me have a few American bees for study, and forthwith they are despatched; and when I desire a copy of some rare or obscure European publication, why, my esteemed friends and correspondents, Doctors Reinhold Meyer, of Darmstadt, and Walther Horn, of the Berlin Museum, courteously oblige me.

"I say the good will existing among the scientists of all nations is the nearest thing to the Universal Brotherhood of Man that this old world possesses. Indeed, the Director of the Berlin Museum has printed in English, on the cover of every scientific paper issued by his institution, the following beautiful expression by Professor Edgworth David of Sydney: "In the world of Science, all men are brothers." What a contrast to the downright selfishness often preached by the politicians in so many lands!"

Not only does Rayment rival Fabre in his keen and persevering powers of observation but he has been more fortunate than the "Homer of the Insects" in his training and in possessing considerable talent as a draughtsman, as shown by the wealth and accuracy of the illustrations which add so much to the excellence of his exposition. His experience of many years as an observant and thoughtful beekeeper was a much better preparation for the study of the native bees of Australia than chemistry. Fabre's long occupation with that science was probably detrimental to his later work as an entomologist, since it seems to have led him to adopt a too schematic formulation of insect behavior. Indeed, it may be doubted whether more than a knowledge of the rudiments of the inorganic sciences is the best preparation for the naturalist as distinguished from the laboratory biologist.

A review of Rayment's volume is difficult, partly because it abounds in so many interesting facts and partly because it may be said to represent a new method of presenting the natural history of a whole fauna. He had the good fortune to take up the study of the Australian bees as a pioneer, with only the very recent, taxonomic contributions of Henry Hacker of Queensland and Professor Cockerell, of the University of Colorado, to serve as an introduction. As he says, "over 100 years of occupation by white people elapsed before a single life-history of a native bee was described" in Australia. And yet the island continent has a rich and, owing to the primitive character of many of its species, a remarkable beefauna. He casually mentions in the legend to one of his figures that 130 species of bees were observed to visit the flowers of a single *Eucalyptus* (*E. calophylla*) at his home near Sandringham, Victoria. Embedded in a wealth of morphological and taxonomic details, but easily separable by the general reader, are fascinating accounts of the bees of great interest to the student of comparative behavior, interspersed with brief disquisitions, or "asides," which rest the reader, on the Australian plants, so unforgettably and wierdly beautiful to those who have encountered them in the field; charming glimpses of the sunny Victorian landscape; short studies of the Ichneumonid and other parasites and enemies of the bees; affectionate mention of helpers and boyfriends; revelations of the author's dislike of city life and of the picnickers and bathers that intrude on his observation grounds along the shores of Port Phillip, and good-natured comments on the politicians and philistines, who, however, are much less numerous and verminous in Australia than they are in the United States.

The longer first part of the volume comprises a number of short essays, each devoted to observations on the structure, life-history and behavior of a species of bee or of some other insect. The bees

are arranged in the usual putative evolutionary sequence, beginning with the very primitive Hylaeidae (Prosopidae) and ending with the social forms (stingless, bumble and honey bees). The Hylaeidae are of unusual interest because they have somewhat similar relations to the higher solitary and social bees as the bull-dog ants (Myrmeciae) to the higher ants and the monotremes and marsupials to the placental mammals. In North America and Europe there are only a few hundred species of the single genus Hylaeus (Prosopis), but about half the Australian beefauna are Hylaeids, belonging to some 15 genera, representatives of all of which have been studied by Rayment. Then follow observations on a number of other primitive solitary bees of the families Colletidae and Andrenidae. Several chapters are devoted to observations on 17 species of *Halictus* (Andrenidae), a cosmopolitan genus, with more than 1000 known species (138 Australian) and of diverse and complicated habits. Although Rayment has devoted an almost unbelievable amount of patient study to these bees and has found that the Australian forms are more primitive than the European in their method of lining their brood cells and in the early disappearance of the overwintering nest-mother, he has been able to elucidate the complete life history of only a few of the species. This is not surprising when we consider that a long series of able European entomologists have held the most diverse views with regard to the number and sequence of annual generations in the same species of Halictus. Rayment finds that some of his species closely resemble those investigated by Fabre, but, unfortunately, he fails to correlate his results with those obtained by the more recent students of the Halicti in Germany—Friese, Blüthgen, Armbruster, Stöckhert, Legewie and, especially, Noll, who in 1931 critically reviewed and clarified the known types of generation-sequence in the European and Chilean species.

The higher solitary bees of Australia belong for the most part to cosmopolitan genera and exhibit only the usual slight specific departures from the typical behavior patterns of their congeners. One species, *Megachile* (*Hackeriaspis*) *deani*, however, shows a surprising innovation in the materials which it chooses for the confection of its cells. Instead of employing cut pieces of green leaves like its ancestors it has taken to making its cells of wax from bee hives. "It is the trade of the creature that has altered. I would remind you, that the doubly-refined white wax, in the form of 'foundation' has been available only since Johannes Mehring invented his press in 1857. Something more than a mere 'reflex machine' is needed to explain this use of an ultra-modern material by a bee that traces its leaf-cutting ancestors back to the Miocene Period (Florissant Shales of Colorado), and, therefore, long before man was evolved to bring utter chaos to his fellow beings." This case, therefore, may be bracketed with the famous cases of the Kea parrot of New Zealand and the Australian blowfly, which have learned to attack living sheep within very recent times.

Only one of the three groups of social Apoidea, the stingless bees (Meliponinae), is native to Australia. It is a purely tropical group with many species in South and Middle America and several in the Ethiopian and Indomalayan Regions. Rayment records 15 species and subspecies, belonging to the genus Trigona, from the warmer parts of Australia and gives us the first comprehensive account of their habits, with illuminating comparisons with the hive bee. There is also a fine chapter on this latter insect. Since there are no Australian bumble-bees, he inserts an account of a European species to fill the gap in the series of social types. Though bumble-bees have been introduced repeatedly into Australia by Rayment and others, they have never survived as they have in New Zealand. He is convinced "that the sole reason for the apparent failure of the bumbles to establish themselves is due to the predatory habits of our birds." The overwintered queens seem to be destroyed by the birds before they can establish their colonies.

One of the most surprising passages in the book is an account of a mysterious honey bee, which Rayment dubs *Apis aenigmatica*, in the sparsely settled moun-

tain regions of Victoria, far from the range of the other species of the genus. He and several of his correspondents have seen the small combs of this bee, which are only three to four inches in diameter and depend from the limbs of trees or other supports. Apparently the insect is now so rare or so nearly extinct that he has been unable to secure specimens of it though he figures the combs. Concerning the cells which are intermediate in size between those of two of the known species of honey-bee, he says:

"Do you remember Darwin's prophecy which he made after viewing a certain flower? He said that a specific moth would be found that fertilized the plant. The forecast proved a correct one. The combs of the five species of *Apis* always prompt me to emulate the great man, and after studying the diagrams, you, reader, will feel as I do. The cells of the giant bee of India [*A. dorsata*] measure about four to the lineal inch; those of the hive bee [*A. mellifica*] five to the inch; while the eastern honey-bee [*A. indica*] constructs six to the same measure. Then there is a hiatus, for the next are those of this Australian bee [*A. aenigmatica*], and which measure nine to the inch, and last, the small cells of the Indian flower-bee [*A. florea*], which builds one more to the lineal measure. I look forward to discovering two new species, whose cells will measure seven and eight to the inch: the sequence will then be unbroken."

Some of the parasitic and other insects, incidentally described by Rayment as he unrolls his remarkable picture of a whole fauna, are quite as interesting as the bees but cannot be adequately reviewed in the space at my disposal. A species of Ichneumonid wasp, however, which copulates with the flowers of orchids in order to ensure their pollination, is too startling to be omitted.

"In January, when the orchids [*Cryptostylis leptochila*] are in their prime, behold, it is not the bees that attract the attention of the observers, but a large, though slender, male wasp, a species distributed over the whole of the Commonwealth and New Zealand, and known to science as *Lissopimpla semipunctata* Kirby. The creature has a reddish head and thorax, but the abdomen is black with a number of pale spots.

I am invited to see for myself the phenomenon of insects effecting a pseudo-copulation with the flowers. But there is no doubt about their actions; the wasps slide down backwards into the flowers, the organs of generation are extruded, the characteristic movements are performed and the seminal fluid is discharged upon the fleshy fold [of the labellum]. It seems inconceivable, but further investigation, and the dissection of several specimens under the microscope, reveals a marvellous correlation between the claspers of the *aedoeagus* and the *vagina* of the flower; there are live sperms in the globule on the tip of the insect's abdomen. Yes, anomalous as it may seem, the sex impulse in the male wasp is excited by the blossom with which it attempts to mate, and in the doing has had glued to its body the pollinia for transportation to another flower.

What obscure laws are responsible for this wonderfully close association? Is the wasp misled by the likeness of bright light on the raised glands of the labellum to the pale abdominal markings of the female, or has the scent of the flower some subtle influence that stirs deeply the sexual instincts of the male? Who knows?

I could go on to relate the absorbing story of another Victorian purple species, the large-tongue orchid, *Cryptostylis subulata*, pollinated by the same wasp, but which has to perform the copulatory action while it is upside-down, but there is no necessity for me to weary you with such additional minutiae."

The first part of Rayment's volume closes with several miscellaneous chapters on the combs and strigils of bees, the neuration of their wings, a classification of the Apoid superfamily, hints to taxonomists and collectors and a series of excerpts on the life-histories of "exotic," that is, non-Australian bees. The second part is purely taxonomic, comprising descriptions of more than one hundred new species, subspecies and varieties of Australian bees and redescriptions of certain forms insufficiently characterized by their authors. The volume contains an adequate index.

The taxonomic portions of Rayment's work will, of course, interest only the specialist, but the portions in larger type will charm the layman no less than the naturalist, and the latter will place the volume in his library among the classic works of Fabre, Wallace, Bates and Belt. It is hardly necessary to add that the "Cluster of Bees" will be an abiding source of inspiration to future students of entomology. The perusal of such contributions sets one to wondering whether the naturalist may not be after all an artist *manqué* or incompletely developed, and not a genuine "scientist." Undoubtedly the activities of the naturalist are to a considerable degree motivated and sustained by esthetic delight in the wonderful forms and colors of animate beings and the intricate temporal patterns, or configurations of their life-histories, behavior and ecological settings. Unlike the "pure scientist" who is devoted to simplicity, the naturalist like the artist, feels at home in the profusion, multiplicity and diversity

of natural phenomena. Lovejoy, in his "Great Chain of Being" (Harvard Univ. Press, 1936), calls attention to these two types of mind, of which I would cite Pascal and Alexander von Humboldt as striking illustrations, when he says (p. 7): "There is, for example, a practically very important difference between (we have no English term for them) *esprits simplists*—minds which habitually tend to assume that simple solutions can be found for the problems they deal with—and those habitually sensible of the general complexity of things, or, in the extreme case, the Hamlet-like natures who are oppressed and terrified by the multiplicity of considerations probably pertinent to any situation with which they are confronted and the probable intricacy of their interrelations." There seems to be a significant resemblance between these simplicist and multiplicist types and the old distinction between Platonists and Aristotelians, between the introverts and extroverts of Jung, the classicists and romanticists of Wilhelm Oswald, the Apollinians and Dionysians of Nietsche, the tender minded and tough minded individuals of William James, the schizothymes and cyclothymes of Kretschmer, the "idéo-émotifs" and "sentimentaux" of Remy de Gourmont, etc. In this connection it may be mentioned that D. C. Peattie's delightful volume, "Green Laurels" (Simon and Schuster, N. Y., 1936) gives an unusually subtle and appreciative insight into the dominant motivation of naturalists.

Perhaps, too, the naturalist's preoccupation with taxonomy has its roots in an unavowed conviction that this "science" is really an art. Nor does his fervid search for truth contradict the foregoing statements, since the artist is quite as much concerned with truth as the scientist, though the naturalist seems to be more desirous of appreciating and understanding than of explaining the phenomena with which he deals. This may account for the non-mathematical and non-experimental spirit in which he approaches and handles his materials. It may also account for his somewhat unsympathetic attitude towards the bright highschool boys now bombinating in the biological laboratories of our universities. He feels that not a few of these neophytes manifest a somewhat gangster attitude towards Nature, so eager are they to assault, scalp or rape her, and so unmindful of the old apothegm, *Natura non vincitur nisi parendo*.

BRIEF NOTICES

EVOLUTION

EVOLUTION.

By A. Franklin Shull. McGraw-Hill Book Co., New York. $3.00. 9 x 5⅞; x + 312; 1936.

This treatise constitutes a general discussion of biologic evolution as interpreted in the light of modern genetic discoveries. The first chapters of the book are given to a clear and detailed presentation of the facts which lead to the concept of evolution; the existence of differences between groups of living creatures, the geographic distribution of species, cytology, genetics, and the known factors of genetic variation. The general conclusions drawn from these facts do not admit of contradiction and form the foundation of modern biology. In the following chapters, which discuss the several theories of natural selection, protective and warning coloration, adaptions, etc., even though the author struggles to find some consistent explanation of the facts and theories, it is evident that the actual mechanism of evolution, the how, why and where, is yet unknown. The exceptional competence of the author and the excellent review of the wealth of facts and theories at his disposition renders this volume interesting and essential not only for students of biological sciences but also for the layman. Throughout the book the author demonstrates a well balanced critical judgment although, in the reviewer's opinion, the neo-Lamarckian theories deserve more attention, at least from the historical standpoint. At times the author's language lacks preciseness; for example, "If only those things were true which have been proven true there would be little verity in the world." (p. 211.) This sentence, if taken literally, would indicate a disregard for scientific method, which we are sure the author has not.

AM WENDEPUNKT DER STAMMESGESCHICHTE. *By Carl Theo Kempermann. Gustav Fischer, Jena.* 1.50 marks. 9¼ x 6¼; 32; 1936 (paper).

The discussion of vitalism and mechanism, although it never comes to any permanently satisfactory conclusion is one that always fascinates biological thinkers. In this pamphlet, the author has arranged the arguments for both sides in compact form. He is thoroughly conversant with the works of Linneaus, Lamarck, Darwin, Haeckel, Dacqué, Smuts, Haldane and others and presents their theories clearly and briefly. He is rather inclined towards a holistic conception of evolution. The work presents no new approach to the problems of evolution, or of mechanism and vitalism, but is intended only as a survey and guide for students.

Происхождение Растении

В. Л. Комаров. Издатедьство Академии Наук СССР, Ленинград. 3 руб. 50 коП.; 192; 1936.

[THE ORIGIN OF PLANTS. *By V. L. Komarov. Publishing House of the Academy of Sciences of U.S.S.R., Leningrad.* 3.50 roubles (paper), 5 roubles (cloth). 9 x 6; 192; 1936].

This little book written by Professor Komarov, member of the Academy of Sciences of U.S.S.R., gives a popular account of the origin of different groups of plants, of their gradual spreading upon terrestrial habitats, and of the evolutionary processes of differentiation of their forms. The style is easy and comprehensible.

GENETICS

HEREDITY AND EVOLUTION. *By Arthur E. Watkins. John Murray, London.* 7s. 6d. net. 7¾ x 5⅛; viii + 243 + 2 plates; 1935.

In this volume the "attitude of genetics towards evolution" is set forth clearly and concisely. It is a book which biological students will find useful, yet it is by no means too formidable for the general reader. The author (University Lecturer in genetics and cytology, Cambridge) discusses the principles of genetics, their scope, the evidence on which they rest, and the bearing of these principles on the theory of evolution. Throughout the text there are figures, graphs and plates, each chapter concludes with a useful list of references and at the end of the volume is given a group of general references, a glossary, and an index.

RÖENTGENOLOGISCHE SKELETTSTUDIEN AN MENSCHLICHEN ZWILLINGEN UND MEHRLINGEN. *Ein Beitrag zu den Problemen der Konstitution und der Phylogenese. Fortschritte auf dem Gebiete der Röntgenstrahlen, Ergänzungsband 46.*

By Franz Buschke. Georg Thieme, Leipzig. 25 marks (paper); 12 x 8½; 47 + 50 plates; 1934 (paper).

X-ray studies were made on the skeletons of 25 pairs of identical twins, 18 pairs of twins of the same sex but not identical, and 7 pairs of male and female twins, and 4 sets of triplets and one set of quadruplets. Form and structure of ossification was very similar among identical twins even to the minutest details, but among ordinary twins there was found to be on the whole less similarity than between unrelated individuals of the same age and sex. However, the authors felt that the number of cases was probably too small to warrant any definite conclusions.

GENERAL BIOLOGY

COLLECTED SCIENTIFIC PAPERS OF SIR WILLIAM BATE HARDY, *Fellow of the Royal Society, Fellow of Gonville and Caius College, Cambridge.*

Published under the Auspices of the Colloid Committee of the Faraday Society. The University Press, Cambridge; The Macmillan Co., New York. $18.00. 10¼ x 7⅛; xi + 922 + 15 plates; 1936.

The collected scientific papers of the late Sir William Hardy enable one to trace a

steady and orderly growth of his interests. A number of excellent accounts have been published of the scientific life of Sir William Hardy, but no better epitome of his aims has been given us than that expressed by Sir Hugh Anderson, the late master of Hardy's College, Gonville and Caius: "Hardy once observed a cell divide under a microscope, and wondered why." The wonder excited in Hardy by the observation of cell division set him on the path of those investigations on physico-chemical properties of the proteins and the behavior of matter in the boundary state. Many believed that, if he had been spared, he would at long last have returned to the problem of why and how a cell divides. This is the key to the plan of his scientific life work, though it represents only one side of his many activities, a side that in the numerous appreciations that have appeared has been little touched on.

The 59 papers, most of them reprinted from the *Journal of Physiology* and the *Proceedings of the Royal Society of London* begin with a developmental study of the hydroid *Myriothela phrygia*, continue with a series of papers on the physiology of leucocytes, and then his central problem becomes the physico-chemical properties of protoplasm. Finally there is a long series of papers on colloids and boundary phenomena. The concluding essay is a statement of the philosophical position of a biologist who sought to advance biology by a well-considered study of non-living systems. The volume is handsomely printed, fully indexed and adequately illustrated with the original lithograph and colored plates. It is altogether a fitting memorial to a remarkable man.

ORDER AND LIFE.

By Joseph Needham. Yale University Press, New Haven. $2.50. 8 x 5⅜; x + 175; 1936.

This volume, by the well known English biologist, is the outgrowth of three Terry lectures delivered at Yale University in 1935. The titles of the lectures are as follows: The nature of biological order; The deployment of biological order; The hierarchical continuity of biological order. Such subjects are discussed as, the unity of natural knowledge; the cleavage between the inorganic and biological sciences, and between the theology of intelligibility and that of inexplicability; the opinions which biologists, physicists and philosophers hold regarding the form of organization which living things exhibit. The author finds that:

> A careful consideration shows us that the fields of morphology and biochemistry are not so sundered as is often supposed. Organising relations are found at the molecular level and at the colloidal and paracrystalline level as well as at the anatomical level. Hardy's work, far from showing that no structure existed in the cell, showed on the contrary how subtle it must be. Although we are still in the earliest historical stages of any far-reaching organisation-calculus, we can yet see that biological order, like (but very much more complicated than) crystal order, is a natural consequence of the properties of matter, and one characteristic mode of their manifestation.

The volume is well illustrated, documented, and indexed. Altogether it is a shrewd and penetrating philosophical summary of the present status of the rapidly advancing frontiers of that broad fundamental field of biology conveniently, if not very precisely, called experimental morphology. But the parsons who administer the money for the Terry lectures must have felt a bit let down by this particular series! Such theological nutriment as may be squeezed out of the lectures is extremely dilute.

INVISIBLE RADIATIONS OF ORGANISMS.

By Otto Rahn. With an Introduction to the Physics of Radiation, by Sidney W. Barnes. Gebrüder Borntraeger, Berlin. 13.20 marks. 8⅝ x 5¾; x + 215; 1936 (paper).

The author summarizes his opinions on this controverted topic as follows:

> The biological part of this book has been written by a biologist who is convinced, from his own experiences as well as from the study of literature, that mitogenetic radiation exists. He has realized that it is difficult to prove it because we are dealing with an extremely weak effect, and with very sensitive detectors. Above all, we are dealing with an entirely new phenomenon, and consequently cannot predict which changes of technique might increase or decrease the effect.

It does not speak well for the present status of science that it has not been possible to settle definitely, in the course of 12 years, the question of the existence of this radiation. The fault lies equally with the two groups of contestants, those for and those against radiation.

The virtue of the book is that it presents clearly and succinctly the important literature, with complete citations, on the mitogenetic problem and its interpretation, and thus houses, in one volume, an ostensibly unbiased account of the subject. After going through the book, however, it seems probable that the reader, although feeling more informed on the many details of the subject, will still be "in the dark" about the plausibility of mitogenetic radiation itself. It is to be hoped that this book will stimulate some conclusive research.

SALINITY AND TEMPERATURE OF THE ENGLISH CHANNEL. *Estimation of Mean Values for the Upper Water Layer over the 25-Year Period 1903 to 1927. Ministry of Agriculture and Fisheries, Fishery Investigations, Series II, Vol. XIV, No. 3.*

By J. R. Lumby. His Majesty's Stationery Office, London. 7 shillings, postage extra. $10\frac{5}{8}$ x $7\frac{1}{4}$; 67 + 3 charts + 83 pp. tables; 1935 (paper).

SALINITY AND TEMPERATURE OF THE ENGLISH CHANNEL. *Atlas of Charts. Ministry of Agriculture and Fisheries, Fishery Investigations, Series II, Vol. XIV, No. 3.*

By J. R. Lumby. His Majesty's Stationery Office, London. 1 shilling, postage extra. 21 x 15; 27 charts; 1935 (paper).

In order to furnish a foundation for future studies in both hydrographical and biological fields especial attention has been given in the preparation and presentation of this report "to the provision of standards embodying as much information as possible, while their representation on charts and their interpretation has been considered as of secondary importance." Fully half of the latter part of the report is taken up with tables in which data are given on (a) The positions allocated to the mean values of temperature and salinity (41 in number); (b) The general mean monthly temperature and salinity, 1903–1927; and (c) The yearly mean temperature and salinity, 1903–1927, together with the general monthly means and the general mean for the whole period. In the first half of the report occur explanatory charts, graphs and tables. There is a list of 41 references.

The group of charts issued separately exhibits the geographical relationship of the means (salinity and temperature) estimated in the above report. There are 12 charts for the months 1903–27 and a figure (same scale as charts) shows the region studied divided into rectangles and regions, and the numerical distribution of the observations.

THE PHENOMENA OF LIFE. *A Radio-Electric Interpretation.*

By George Crile. Edited by Amy Rowland. W. W. Norton and Co., New York. $3.50. $8\frac{1}{2}$ x $5\frac{3}{4}$; 379; 1936.

The radiations emitted by this volume have the following characteristics, as stated by the author:

We shall offer evidence tending to show that the living organism is specifically adapted to the formation, storage and specific use of electric energy and that the genesis of this electric energy is due to radiant energy emitted by ultramicroscopic units or furnaces in protoplasm. These furnaces we have called *radiogens*. We shall postulate that the combustion of the proteins is effected by these microscopic units and that the short wave radiation emitted by this continuous combustion has two primary and fundamental effects. (1) Short wave radiation knocks off electrons and thus disturbs the electrical state of the protoplasm, especially of the infinitely intricate network of the nervous system. (2) Short wave radiation so disturbs the architecture of the atom as to make the atoms chemically active, thereby forming the basis for the synthesis of protoplasm.

It seems to us unlikely that any professional biologist will regard the evidence presented as establishing the conclusions reached. In fact this book considerably increases the conviction engendered by the author's earlier excursions into the realm of theoretical biology that, as a biologist dear Dr. Crile is a great surgeon.

PROBLEME DER THEORETISCHEN BIOLOGIE. *Arbeiten aus dem Timirjaseff-Institut für Biologie—Moskau.*

Herausgegeben zum 15. Todestag von K. A. Timirjaseff. INRA Verlagsgenossenschaft, Moskau-Leningrad. 7 x 10; 409; 1935 (cloth). No price.

This volume is dedicated to the memory of Professor Timirjaseff, a well-known Russian plant physiologist who has also contributed much by his writings and translations to the wide-spread recognition of Darwinism in Russia of the past century. He was a foreign member of the Royal Society and delivered a Croonian Lecture in 1903. In this volume a number of papers issued from the Institute bearing his name is published in German, and thus made available to wider circles of readers. There are papers by Professor Navaschin on 'The Nature of Mutations', by Professor Tokin on regeneration, and many other contributions.

PROTOPLASM.

By William Seifriz. McGraw-Hill Book Co., New York. $6.00. 9 x 6; x + 584; 1936.

A book for students in biology and medicine and the related fields of biochemistry and biophysics. The author has brought together "all those parts of the branches of science which bear upon the physical chemistry of living matter." This means that a great deal of rather technical matter, particularly mathematical, had to be included, but the author has done this with considerable skill and the volume is not too formidable for second year students. Particular attention has been given to colloid chemistry. The volume has many illustrations and is well documented and indexed.

URDEUTSCHLAND. *Deutschlands Naturschutzgebiete in Wort und Bild. Lieferungen* 15, 16, 17, 18, 19.

By Walther Schoenichen. J. Neumann, Neudamm. 2 marks each. $10\frac{3}{4}$ x $8\frac{1}{4}$; Lief. 15, 49–72 + 9 plates; Lief. 16, 73–96 + 9 plates; Lief. 17, 97–120 + 9 plates; Lief. 18, 121–144 + 9 plates; Lief. 19, 145–168 + 9 plates.

Five numbers of this beautifully produced and illustrated work on the natural history of Germany, earlier numbers of which have been noticed in successive numbers of this REVIEW beginning with Volume 10, Number 3.

HUMAN BIOLOGY

A HUNDRED YEARS OF ANTHROPOLOGY.

By T. K. Penniman. The Macmillan Co., New York. $4.50. $8\frac{1}{2}$ x $5\frac{3}{8}$; 400; 1936.

A book of great usefulness and interest. It is divided into the *Formulary period* (before 1835) "when the elements of the science are scattered throughout all the others;" the *Convergent period* (1835–59) "when efforts are made to relate the various sciences that bear on Man, ending with the admission of the high antiquity of palaeolithic man and the publication of *The Origin of Species* in 1859;" the *Constructive period* (1859–1900) which "shows a steady and confident development for the most part on evolutionary lines;" and the *Critical period* (1900–1935) when the "rediscovery of Mendel's work in 1900 introduced a more austere and critical mood," and more intensive and special research entered all branches of anthropology. The author, who is Secretary to the Committee for Anthropology in the University of Oxford, has done his work well. A general map is all that he has aimed to lay before the reader but it is clearly drawn and in the main furnishes a well balanced survey of this rapidly advancing branch of science. The general reader as well as the student will find it absorbing. There is a final section on the future of anthropology, appendixes on (1) A chronological list of men and events in the history of anthropology; and (2) Some principal congresses, anthropological museums, societies, and periodicals in various countries of the world; a lengthy bibliography and an index.

CRITERIA FOR THE LIFE HISTORY. *With Analysis of Six Notable Documents.*

By John Dollard. Published for the Institute of Human Relations by Yale Univer-

sity Press, New Haven. $2.50. 9 x 9; v + 288; 1935.

The author defines *life history* as "an account of how a new person is added to the [social] group and becomes an adult capable of meeting the traditional expectations of his society for a person of his sex and age." The use of life histories as a method of investigation in social psychology has been adopted only recently since some sociologists have realized, at last, that an understanding of human social relationship can only be obtained by actually studying the individual and his reactions to his particular social environment. In order to arrive at a standard method of analysis the author proposes seven criteria which he considers essential for an adequate life history. They are:

I. The subject must be viewed as a specimen in a cultural series.
II. The organic motors of action ascribed must be socially relevant.
III. The peculiar rôle of the family group in transmitting the culture must be recognized.
IV. The specific method of elaboration of organic materials into social behavior must be shown.
V. The continuous related character of experience from childhood through adulthood must be stressed.
VI. The "social situation" must be carefully and continuously specified as a factor.
VII. The life-history material itself must be organized and conceptualized.

He then applies these criteria to seven well known biographic and autobiographic documents, one each from A. Adler, J. Taft, S. Freud, W. I. Thomas and F. Znaniecki, C. R. Shaw, H. G. Wells, P. Radin. The author's penetrating comments on these documents are interesting and indicate that, as he uses them, the criteria should prove helpful toward an objective study of individual social behavior. It is well to note, however, that this method is decidedly unilateral because while it describes the influence of the social group on the individual it apparently fails to take into account the fact that the individual does not remain passive but in turn exerts some influence on the group.

COSTITUZIONE E MORTALITÀ. *Pubblicazioni della Università Cattolica del Sacro Cuore. Serie Ottava: Statistica. Vol. X.*

By Alessandro Costanzo. "Vite e Pensiero," Milano. 15 lire. 10 x 6½; ix + 187; 1936 (paper).

The investigation here reported adds more evidence to that already collected regarding the diverse morbidity and mortality of individuals with different somatic constitutions. The material consists of the anthropometric data recorded for some 9000 Italian military conscripts who were born at or near Casale di Monferrato during the years 1845 to 1864, 1865 to 1880 and 1881 to 1910. The measurements of stature and chest circumference were those obtained at the medical examination to which all Italians at or around 20 years of age must be subjected in order to determine their fitness for military duty. The material is therefore unselected, and homogeneous with regard to sex, race and age. The author has investigated the ages and causes of death of these individuals. The results definitely confirm the findings of other students of the subject.

The distribution of individuals according to age at death shows that the younger dead were, on the average, those who at 20 had been of more slender build. Those dead of tuberculosis and lower respiratory infections were those who at 20 had been more slender, while those who died of circulatory and gastro-intestinal diseases were those who at the time of examination had been stocky.

The value of this study lies essentially in the fact that the material is a random sample of the population. It is to be deplored that more complete anthropometric data are not available. The biometric analysis is above reproach, but the grouping of circulatory diseases with those of the gastro-intestinal tract deserves criticism.

ABORTION—*Spontaneous and Induced. Medical and Social Aspects.*

By Frederick J. Taussig. The C. V. Mosby

Co., St. Louis. $7.50. 9¾ x 6¾; 536; 1936.

The object of this monograph is: (1) to present a critical outline of the methods of diagnosis and treatment of the various forms of abortions and (2) to discuss the consequences of the legal restrictions regarding the performance of abortions. As for contraception in general and for venereal diseases, the moral and religious taboos of our civilization persist in hampering the thoughts and actions of the medical and sociological investigators of the subject. It is deplorable, as the author notes, that while apparently one out of every three or four pregnancies terminates in an abortion, the textbooks on obstetrics dedicate relatively little space to the treatment of this condition which, it is estimated, causes about 10,000 deaths of mothers yearly in the United States alone. To remedy this deficiency Professor Taussig discusses in full the anatomy and physiology of early pregnancy; the etiology, mechanism and pathology of abortion, and the symptoms, signs and methods for its diagnosis. In the following chapters he describes the several operative techniques and the advantages to be derived from each. This part is closed with a section on the complications and sequelae of abortion. There is an extensive bibliography and numerous and excellent photographs. For the human biologist the main point of interest lies in the discussion of the religious and legal taboos and how these have persisted to our day. Included is also a chapter in which the author describes his visit to a Russian abortarium.

The book closes with a plea for greater latitude in the teaching of contraceptive methods. This, the author hopes, will decrease the number of illegally produced and self-induced abortions and their harmful results. We doubt the success of such a plea, for the moralists who decry the use of both contraceptives and abortions have never been swayed by the suffering of mere mortals.

WER IST ERBGESUND UND WER IST ERBKRANK? *Praktische Ratschläge für die Durchführung des Gesetzes "zur Verhütung erbkranken Nachwuchses" und zur Verleihung der Ehrenpatenschaft.*

Edited under the auspices of Berliner Akademie für ärztliche Fortbildung by W. Klein. Gustav Fischer, Jena. 6.50 marks (paper); 8 marks (cloth). 9¾ x 6⅛; xviii + 215; 1935.

Sterilization laws naturally bring up many problems and much discussion, especially as to judgments on who should be sterilized and who allowed the pleasure of engendering future citizens. Hitler's edict of July 14, 1933 was no exception. In this book are published thirteen lectures by prominent physicians and geneticists delivered at the Berlin Academy for Medical Progress on topics pertinent to this subject as to the inheritance of various diseases and anomalies. On the whole they present a good summary of what is known, and what isn't, about the genetic transmission of disease, and most of the conclusions drawn are quite sound. However, some seem to us a little extreme, and one cannot help but wonder what would happen to the birth-rate if wholesale sterilization of persons suffering from some such discomfort as impairment of hearing should come into effect. Prefaced by extracts from the Sterilization Law and an Introduction by W. Klein, the topics and authors are as follows: Demographic-political measures in the Third Reich, by W. Klein; Foundations of genetics, by v. Verschuer; Disease of the heart and blood vessels, kidneys and blood-forming organs, by W. Weitz; Metabolic disease, diseases of the stomach, intestines and liver, and cancers, by F. Curtius; Diseases of the respiratory organs and tuberculosis, by K. Diehl; Nervous diseases, by W. Bremer; Mental diseases, by J. Lange; Diseases of the eye, by C. Adam; Diseases of the ear, by H. Claus; Children's diseases, by G. Bessau; Gynecological diseases and disturbances of the physiological functions of the woman, by G. A. Wagner; Skin diseases, by H. Gottron; Physical defects, by L. Kreuz.

ANTHROPOLOGIE STŘEDOAFRICKÝCH PYGMEJŮ V BELGICKÉM KONGU. *Anthropology*

of the Central African Pygmies in the Belgian Congo.

By Paul Schebesta and Victor Lebzelter. Czech Academy of Sciences and Arts, Prague. 14¼ x 10½; 144 + 56 plates; 1933 (paper).

In 1929–30, the senior author conducted an expedition to the Belgian Congo for the express purpose of studying the physique of the pygmies of that region. In this report, written in both Czech and English, he presents the detailed individual measurements and somatic descriptions of the subjects, and notes regarding their social status, sex, age, and certain disease conditions. These data have been statistically summarized by the junior author. Dr. Schebesta arrives at the conclusion that most of the pygmies of this region belong to one racial group, the Bambuti; a few only show some mixture of European and Negro blood. The Bambuti are characterized by a disproportionately large head, long trunk and long, thin arms, short neck and short, thin legs, slender feet and hands. The complexion is greyish yellow, the growth of face and body hair is generally heavy. The maximum stature, observed in male adults, is less than 160 cm.; the minimum, 118 cm., is that of an adult female, mother of a fully developed six year old child. This monograph is illustrated by numerous and excellent photographs. These, together with the detailed data, will be found extremely useful by the reader, especially since the statistical treatment of the data is rather inadequate.

OUT OF THE NIGHT. *A Biologist's View of the Future.*

By H. J. Muller. The Vanguard Press, New York. $1.50. 7½ x 5; 127; 1935.

The author of this volume is at present serving as Senior Geneticist at the Institute of Genetics of the Academy of Sciences in Moscow. Most of the material in the book was given in a series of lectures at the University of Chicago in 1925, under the title "A Biologist's View of Progress." Section 6 (Heredity and Characters) has been since added. The central theme of the book "lies in the attempt to show that for a continuance of material, cultural and biological progress in the human race, a thorough-going economic and social change to a more truly coöperative basis of society, together with the regeneration in human motivation attendant upon this is a prior necessity." Great stress is laid on the "possibility of positive biological improvement of mankind, *provided* the social reconstruction occurs first." In the final section are set forth the author's views on the improvement of the human race by artificial insemination. The volume is without index.

VOYAGE TO GALAPAGOS.

By William A. Robinson. Illustrated by Daniel T. West. Harcourt, Brace and Co., New York. $3.00. 8 x 5¼; viii + 279 + 8 plates; 1936.

The Galapagos Islands figured prominently in the newspapers two or more years ago when the author of this volume was taken seriously ill in Tagus Cove with appendicitis. This is the story of the voyage that ended so disastrously. There were three on the little Svaap. From almost the beginning they found themselves in the midst of excitement—dangerous storms, a shipwreck in the jungles of Darien, and endless delays in relaunching the boat. They reached the Galapagos Islands soon after the sensational events among the little group of self-exiled Europeans, ruled by the self-appointed Empress of Galapagos, occurred. Robinson gives his version of this fantastic tale and a possible explanation of the mysterious disappearance of some of these people. The reader gets an interesting picture of the Inca coast, the Humboldt current, the Guano Islands and their bird life, and animal life in the Galapagos. The volume is illustrated but without index.

STUDIES OF THE YAQUI INDIANS OF SONORA, MEXICO. *Texas Technological College Bulletin, Vol. XII, No. 1. Scientific Series No. 2.*

By W. C. Holden, C. C. Seltzer, R. A. Studhalter, C. J. Wagner and W. G.

McMillan. Texas Technological College, Lubbock. 60 cents postpaid. 9 x 6; 142; 1936 (paper).

During 1934 two expeditions organized at Texas Technological College proceeded to the lower reaches of the Rio Yaqui in northwestern Mexico for the purpose of studying the Yaqui Indians living there in eight historic villages. In this paper W. C. Holden, anthropologist and director of the expedition, has reported on social organization, marriage, child rearing and education, *La fiesta de gloria*, Yaqui funerals, and household economy; C. C. Seltzer, physical anthropologist of Harvard, contributed an article on "Physical characteristics of the Yaqui Indians"; C. J. Wagner, a physician, writes on "Medical practices of the Yaqui"; R. A. Studhalter, biologist, on "Yaqui agriculture," and W. G. McMillan on "Yaqui architecture." These articles with the exception of Dr. Seltzer's, were written primarily for the layman rather than the professional anthropologist.

LAWS OF LIFE.

By Halliday Sutherland. Sheed and Ward, New York. $2.50. 7¼ x 5; v + 270; 1936.

Dr. Sutherland is a well known Catholic. He tries very hard to defend his ideas on sex and population by pure logic, but his religious opinions are always evident and his biblical quotations numerous. He is opposed to contraception, sterilization and euthanasia. The "safe period" is advocated as the best biological, moral and aesthetic form of birth control. Dr. Sutherland has long been interested in population problems, and includes in this book a brief chapter on the logistic curve.

All in all "Laws of life" seems to us a slightly too ambitious title for a collection of not wholly unbiased opinions on a variety of biological and sociological problems.

SOUTH SEAS.

By Hugo A. Bernatzik. Translated from the German by Vivian Ogilvie. Henry Holt and Co., New York. $3.50. 9 x 6; xiv + 167 + 103 plates; 1935.

An interesting, well written popular account of various peoples and places in the Solomon Islands, New Guinea, and Bali, by a distinguished Austrian anthropologist, beautifully illustrated with over a hundred rotogravure plates from original photographs. While the author's intention in the book is popular entertainment rather than technical science, there are a good many shrewd observations and discussions relating to significant problems, such as depopulation. Making no great pretension the book as a whole is excellently done, and can be warmly recommended for the intelligent gentleman's library, the transatlantic voyager's book hamper, or even the summer vacation hammock.

THE MEASUREMENT OF POPULATION GROWTH. *Methods and Results.*

By Robert R. Kuczynski. Oxford University Press, New York. $4.00. 8½ x 5⅜; vi + 255; 1936.

The author surveys a few of the methods proposed for the measure of fertility and population growth. He violently criticizes all of them except the gross and net reproduction rates which *he* uses and discusses at length here, as in his previous publications. His criticism is more bitter than fair since he neglects to mention that some of those indices, the use of which he censures, were not constructed for the purpose of answering the specific questions which he asks of them. The author makes much of the fact that these indices are based on census and vital statistics data, often inaccurate. The deficiencies of such data are well known to all students of population problems and the author apparently forgets that they also affect the indices which he uses. There is an appendix with useful population data for a number of countries.

DIE HAND UND IHRE GEHEIMNISSE.

By Adolphe Desbarolles. Otto Wilhelm

Barth, München-Planegg. 6 marks (paper); 7.50 marks (cloth). 8⅝ x 5½; 313; 1935.

This translation from the works of the Frenchman, Desbarolles, who lived in Paris 1804–1866, is chiefly a plea for the reëstablishment in the scientific world of the old arts of phrenology, graphology, chiromancy, and astrology. Nothing new is brought forward, the old arguments are only dressed up in new language.

Desbarolles got his start in chiromancy during a visit in Spain, when he associated with gypsies, and learned their formulae for palmistry. The book is well documented, and ought to be interesting to those for whom palm reading is a never ending source of fascination.

DESOLATE MARCHES. *Travels in the Orinoco Llanos of Venezuela.*

By L. M. Nesbitt. Harcourt, Brace and Co., New York. $2.50. 8 x 5¼; 320; 1936.

An interesting account of travels and adventures incidental to engineering development work in a part of Venezuela not commonly visited. The country traversed is not very exciting, and extremely trying climatically. The two chief impressions left by the book are the rankness of tropical vegetation in the atmosphere of a super-hot and super-humid green house, and the gradual but steady deterioration of the population living in such an environment.

RASSENKUNDLICHE BESTIMMUNGS-TAFELN *für Augen-, Haar- und Hautfarben und für die Iriszeichnung.*

By Br. K. Schultz and M. Hesch. J. F. Lehmann, München. 16 marks (in Germany); 12 marks (outside Germany). 3 colored and 1 black and white chart in folder 6¾ x 5½ inches. No date.

This collection of hair, skin and eye color charts is in our opinion not a particularly good one. The difficulty of making such charts cannot be over-estimated, but ten shades of hair coloring seems hardly adequate. The attempt to show patterns of eye pigmentation is interesting, but typical drawings might have been preferable to photographs.

TOMORROW'S CHILDREN. *The Goal of Eugenics.*

By Ellsworth Huntington, in conjunction with the Directors of The American Eugenics Society. John Wiley and Sons, New York. $1.25. 8 x 5½; x + 139; 1935.

This book, written for the layman, explains the main principles of eugenics and their application to social problems. The material is clearly presented and many aspects of eugenics are considered. We feel, however, that the question and answer form could have been dispensed with. There is a classified bibliography and a good index.

A BIBLIOGRAPHY OF SIR JAMES GEORGE FRAZER, O. M.

Compiled by Theodore Besterman. The Macmillan Co., New York. $4.50. 8½ x 5⅜; xxi + 100 + 3 plates; 1934.

Published on the eightieth anniversary of Sir James George [Golden Bough] Frazer's birth, this volume gives a complete bibliography of his work in chronological order. There is also a classified list and an alphabetical index. The work is well done, and will serve a useful purpose.

MEN IN SUN HELMETS.

By Vic Hurley. E. P. Dutton and Co., New York. $2.50. 8⅛ x 5½; 252; 1936.

A realistic and interesting account of life in the Philippines. The author shows the danger, discomfort and monotony of the tropics as well as the romance.

BULLETIN DER SCHWEIZERISCHEN GESELLSCHAFT FÜR ANTHROPOLOGIE UND ETHNOLOGIE 1935/36. *12 Jahrgang.* [*Bulletin de*

la Société suisse d'Anthropologie et d'Ethnologie 1935/36. *12me année*].

Siège de la Société, Institut anthropologique de l'Université, Plattenstr. 9, Zurich 7. 9 x 6¼; 20; 1936.

ZOÖLOGY

OCEANIC BIRDS OF SOUTH AMERICA. *A Study of Species of the Related Coasts and Seas, Including the American Quadrant of Antarctica Based Upon the Brewster-Sanford Collection in the American Museum of Natural History. Vols. I and II.*

By Robert C. Murphy. Illustrated from Paintings by Francis L. Jaques. American Museum of Natural History, New York. $10.50 per set. 10¼ x 7¾; xxiii + 1245 + 72 plates; 1936.

During the years 1912–1917 the Sanford-Brewster expedition under the direction of Mr. Rollo H. Beck made the first organized trip of its kind around South America to undertake a systematic field study of sea birds. In these volumes Dr. Murphy has ably organized and presented the great wealth of data accumulated as a result of this expedition. He has also incorporated material from various other sources which would aid in giving a greater completeness to the study.

Part I (first half of Volume I), prefaced with a brief narrative of the Brewster-Sanford expedition, is given to the consideration of the physical environment of the regions—geographic background and hydrology in relation to oceanic birds. Part II (last half of Volume I and all of Volume II) is devoted to the life histories of some 183 species and subspecies of oceanic birds. The selection of species and forms for consideration in these biographies was based upon geographical criteria rather than blood relationship. The forms chosen fall ecologically into the four groups of littoral, inshore, offshore and pelagic birds. Two forms are described as new in this book. The nomenclature of Peter's *Check-List* has been used.

Eighty text figures, 16 colored plates, 72 photographs, a bibliography and index complete these carefully prepared and valuable volumes.

LAND OF ELEPHANTS. *Big-Game Hunting in Kenya, Tanganyika and Uganda.*

By Count Zsigmond Széchenyi. Putnam and Co., London. 12s. 6d. net. 8½ x 5½; xi + 209 + 96 plates; 1935.

AFRICAN ADVENTURE. *Letters from Famous Big-Game Hunters.*

Edited and Annotated by Denis D. Lyell. E. P. Dutton and Co., New York. $3.75. 8½ x 5½; xv + 270 + 8 plates; 1935.

Both these books deal with hunting adventures and exploits in Africa; Count Széchenyi's in Kenya, Tanganyika, and Uganda in the immediate past; Mr. Lyell's over a wider field and time. Both will be enjoyed by all sportsmen, naturalists, and students of animal behavior.

Count Széchenyi is a young and handsome Hungarian nobleman devoted to big-game hunting and life in the wild. His book is made up of extracts from his field diaries; episodic rather than continuing narrative. Its most noteworthy feature is the large number of photographs reproduced as half-tone plates. The author was nearly or quite as much interested in photography as in shooting. Some of the lion pictures are quite extraordinary. Of particular interest to biologists is the picture of a herd of zebra, showing the camouflaging effect of the pattern as distance increases. There is a long and interesting chapter on termites, based upon the work of Escherich and to some slight extent on the author's own observations.

Mr. Lyell's book is made up of letters that he has received from famous big-game hunters, mostly British, interlarded with his own comments upon points suggested by the letters. These comments and annotations are always shrewd, and on the whole more interesting than the letters, many of which it must be confessed are a bit dull and trivial. Mr. Lyell is a Scot of vast experience in African big-game hunting, and a practical kind of person. Anyone making a first hunting trip to Africa will make a mistake if he does not take this book along and ponder over the wisdom it contains.

PROCEDURE IN TAXONOMY. *Including a reprint of the International Rules of Zoölogical*

Nomenclature with Summaries of Opinions Rendered to the Present Date.

By Edward T. Schenk and John H. McMasters. Stanford University Press, Stanford University, Calif. $2.00. 9 x 6; viii + 72; 1936.

"This book was prepared for the purpose of supplying the student as well as the professional systematist with (1) a clear-cut and comprehensive statement of the principles of taxonomy; (2) the International Rules of Zoölogical Nomenclature; (3) Summaries of Opinions rendered to the present date; (4) a complete index—the only index of the rules and summaries ever published." Many readers will be surprised by the technicalities and legal aspects offered by the field of taxonomy. Much of the book reads like a textbook on torts. One list, which the reviewer found both interesting and alarming, consisted of a series of terms used in describing zoölogical groups of various degrees and kinds. At the risk of some tedium this list is appended: "Aberration, blastovariation, branch, class, cohort, conspecies, division, family, form, gens, genus, jordanon, kingdom, legion, morpha, mutation, nation, order, phalanx, phratry, phylum, proles, race, section, series, species, subclass, subfamily, subgens, subgenus, subkingdom, suborder, subphylum, subspecies, subtribe, subvariety, superclass, superfamily, superform, supergenus, superorder, supertribe, supervariant, supervariety, tribe, variant, variety." This, as the authors say, is only a "partial" list!

OUR ENEMY THE TERMITE.

By Thomas E. Snyder. Comstock Publishing Co., Ithaca, N. Y. $3.00. 9 x 6; xii + 196; 1935.

Dr. Snyder is probably better fitted to write a book of this type than any other man working in the field today as his experience has taken him into all the phases of termitology since his early association with Dr. Nathan Banks more than twenty-five years ago. The book discusses termites from the earliest known fossil forms to those of the present day; their biology, behavior, structure, and extermination. Fortunately the author has been in close touch with all these phases, both in the United States and in several tropical countries. The reader is introduced into the field of termite control by such methods as wood preservation, building codes, poisons, and biological control. One easily grasps the notion that the termite problem actually is on the increase in many locations due to conditions created by man which are especially favorable to termite increase. Dr. Snyder's dissertation on anthropocentricism should be read by everyone who endows the social insects with supernatural powers. The book will serve as a good antidote for the works of Maeterlinck and other romantic biologists.

MAMMALS OF INDIANA.

By Marcus W. Lyon, Jr. American Midland Naturalist, University of Notre Dame, Notre Dame, Indiana. $3.00. 9 x 5⅞; 384; 1936.

The material appearing in this book is reprinted from the "American Midland Naturalist" and is an attempt, " . . . to bring up to date the main facts of the mammalian fauna of Indiana and make them available in a single volume without recourse to the published writings of others more or less hidden away in serial publications containing other matters."

The mammals are taken up systematically starting with the opossum and ending with Jefferson's ground-sloth. For each species discussed, data are given about the taxonomic synonomy; the general geographic range including the local Indiana records; the description of the form; the ecologic habitat; the breeding activities, and other miscellaneous items. There are several taxonomic keys which should prove useful and a number of maps reporting the distribution of the species in question throughout the various counties of the state. An extensive bibliography is also appended.

The book has been prepared in a workmanlike manner and should prove of considerable service to mammalogists of Indiana and adjoining states.

THE MIGRATION OF NORTH AMERICAN BIRDS. *United States Department of Agriculture Circular No. 363.*

By Frederick C. Lincoln. U. S. Government Printing Office, Washington. 10 cents. $9\frac{1}{8}$ x $5\frac{7}{8}$; 72; 1935 (paper).

The extensive program of bird-banding carried on by the Biological Survey for many years has resulted in important records bearing on bird migration, and this pamphlet is a very successful presentation of the major results for the benefit of biologists and bird lovers. Numerous maps show the areas in which certain species of birds spend the breeding season, areas in which they winter, and routes they follow in migration, while isochronal lines show approximately the time consumed in migration. The theories advanced to account for bird migration are summarized briefly, additional facts are presented and a few generalizations are expressed. A bibliography and an excellent index, listing both English and Latin bird names, help to make this a most useful publication for everyone interested in birds.

HUNTING WILD LIFE WITH CAMERA AND FLASHLIGHT. *A Record of Sixty-five Years' Visits to the Woods and Waters of North America. Vol. I. Lake Superior Region. Vol. II. Wild Life of Coasts, Islands, and Mountains.*

By George Shiras, 3d. National Geographic Society, Washington. $5.00 the set. 10 x $6\frac{3}{4}$; Vol. I, xxi + 450; Vol. II, viii + 450; 1935.

George Shiras, 3rd, author of these two beautiful volumes of portrait and word pictures of wild life in North America, was the originator of flashlight photography of wild animals, a technique that he has developed into a fine art. The reproductions here of 950 of his fine photographs can leave no one in doubt as to the high degree of perfection this art has reached during his many years of persistent endeavor to make hunting with the camera a sport not to be excelled by that of hunting with a gun. The book is published by the National Geographic Society, in whose magazine much of the text and many of the photographs of these volumes have appeared over a period of years. Volume I is concerned with the wild life of the Lake Superior region, and Volume II with the wild life of coasts, islands and mountains. There is an index to Volume II, but none to Volume I.

EIN LEBEN FÜR TIERE.

By Johannes Gebbing. Bibliographisches Institut AG., Leipzig. 5.80 marks (25 per cent reduction outside Germany). 9 x $6\frac{1}{4}$; 290 + 65 plates; 1936.

In addition to Gebbing's autobiography and a history of the development of the Leipzig Zoo during the past 25 years under the author's directorship, this book contains much interesting material on the life and behavior of animals in their native habitats, in the zoo, and in the films and circus. The author writes from first-hand knowledge. He himself took part in the expeditions to collect what is reputed to be the largest collection of lions in any zoo, and also other animals, and was not averse to hiring out both some of the animals and himself to cinema companies and circus arenas during the war and inflation years to raise money for the up-keep of his collection. An interesting book, nicely illustrated, mostly with animal portraits.

THE MIGRATIONS OF ANIMALS FROM SEA TO LAND.

By A. S. Pearse. Duke University Press, Durham, N. C. $3.00. $8\frac{1}{2}$ x $5\frac{1}{2}$; x + 176; 1936.

In this book an attempt is made to condense the available facts bearing on the migrations of animals from sea to land. One chapter is devoted to the principal routes of migration, one to the causes of these migrations, and one to changes which animals have undergone in their movement from sea to land. The method of presentation is somewhat novel and in several cases (e.g., the salmon and soft shelled clam) not entirely consistent with facts. It seems regrettable that more

time could not have been given to a wider appreciation of certain important topics so that the review included in the text might give a clearer and more accurate picture to the student. The bibliography includes over 700 references and represents one of the best features of the book. The volume is recommended to students interested in physiological ecology and marine biology.

PRÉCIS DE BIOLOGIE ANIMALE. *A l'Usage des Candidats au Certificat d'Études Physiques, Chimiques et Biologiques et a la Licence ès Sciences.*

By M. Aron and P. Grassé. Masson et Cie, Paris. 80 francs. $7\frac{5}{8}$ x $5\frac{1}{4}$; viii + 1009; 1935.

This is a French zoölogical text prepared, "A l'usage des candidats au certificat d'études physiques, chimiques et biologiques et à la licence ès sciences." It differs not fundamentally in organization from the many similar books in English which devote about half of their space to a discussion of biological principles—structure and function of protoplasm, cytology and heredity, general physiology, ecology, etc.—and the remaining half to a systematic review of the animal phyla. The book has the virtues of clear organization, numerous drawings, and an extensive index and table of contents. It is typographically superior to the usual run of French textbooks.

A GUIDE TO HUMAN PARASITOLOGY *for Medical Practitioners. Second Edition.*

By D. B. Blacklock and T. Southwell. William Wood and Co., Baltimore. $4.00. $9\frac{1}{4}$ x 6; viii + 259 + 2 plates; 1935.

This book on practical parasitology for the clinician (previously reviewed in Q. R. B., Vol. 8, p. 232) has been revised slightly in its second edition by the omission of certain material which the authors felt "incapable of adequate treatment in an elementary textbook of this nature." Comparison of the table of contents of the two editions shows that the omitted material, totalling eleven pages, concerned itself with the drugs used in the treatment of certain of the diseases discussed in the text.

INTRODUCTION TO HUMAN PARASITOLOGY. *Fifth Edition, Rewritten and Enlarged.*

By Asa C. Chandler. John Wiley and Sons, New York. $5.00. 9 x $5\frac{3}{4}$; xvi + 661; 1936.

This successful and important textbook has been revised in its fifth edition by the inclusion of new material in the chapters dealing with the spirochaetes, amoebae, malaria, rickettsias, flukes, Strongyloides, filariae and myiasis; by alteration of the arrangement and organization of certain of the chapters with the view of making them easier for students to follow, and, by making a few changes in nomenclature and classification. Brought up to date as it is, it should continue to serve students of general human parasitology. There is a short bibliography and an index.

UNTERSUCHUNGEN ÜBER DIE TIERWELT DES WIESENBODENS.

By Gerhard Frenzel. Gustav Fischer, Jena. 6 marks. $9\frac{1}{4}$ x $6\frac{1}{4}$; v + 130; 1936 (paper).

The data concerning the metazoa found in the meadow-lands of Germany described in this book include: distribution, population density in different localities and at different seasons, life histories, type of soil, soil temperature, depth at which the metazoa were found, etc. Several varieties of Nematoda not previously described for Germany are included. Bibliography and author and subject indices are provided.

AN AVIARY ON THE PLAINS.

By Henry G. Lamond. Angus and Robertson, Sydney. 6 shillings. $7\frac{1}{4}$ x $4\frac{3}{4}$; viii + 228; 1934.

This book records the observations of a non-scientific bird lover on the birds inhabiting a hypothetical aviary in Australia lying between the 137th and 139th degrees of longitude and the 20th and 22nd

degrees latitude. The interspersion of numerous contractions and colloquialisms such as 'em for "them," "the old girl" in designating a female bird, etc., will be irritating to those who enjoy a different type of English, and will insofar detract from the pleasure one might derive from these otherwise rather pleasing descriptions of bird life. The book has no index.

A Natural History of the Seas.
By E. G. Boulenger. D. Appleton-Century Co., New York. $3.00. 8½ x 5½; 215 + 9 plates; 1936.

The author, Director of the London Zoological Society's Aquarium, has written a book for the general reader. He has made a survey of the teeming populace of the ocean, pointing out the various groups, and describing with considerable detail some of the more interesting members of the groups. The numerous sketches and photographs will help the reader to recognize these forms readily wherever he may come upon them. The volume is indexed.

Report on the Maldon (Essex) Periwinkle Fishery. *Ministry of Agriculture and Fisheries. Fishery Investigations, Series II, Vol. XIV, No. 6.*
By F. S. Wright. His Majesty's Stationery Office, London. 2 shillings. 10½ x 7¼; 37; 1936 (paper).

This report embodies a valuable review of information on the natural history of the intertidal gastropod *Littorina littorea* and allied species as well as certain original contributions to our knowledge of the abundance, rate of growth, and the practical aspects of the fishery of *Littorina littorea* in the region of Maldon (Essex), England.

Die tierischen Parasiten *der Haus- und Nutztiere, sowie des Menschen. Ein Lehr- und Handbuch mit Bestimmungstabellen für Tierärzte, Ärzte und Studierende. Dritte, umgearbeitete Auflage.*
By Josef Fiebiger. Urban und Schwarzenberg, Berlin. 17.50 marks (paper); 19 marks (cloth). 10 x 7; xii + 375; 1936.

The third edition of a well known and widely used text on animal parasitology. The book is divided into two sections. Part I deals with general descriptions of parasites, their life cycles, hosts, etc. Part II is a detailed classification and description of the different groups of parasites. The book is well illustrated.

Report on Investigations into the Conditions of Certain of the Oyster Beds in the South Wales Sea Fisheries District (*June, 1934*). *Fishery Investigations, Series II, Vol. XIV, No. 5.*
By F. S. Wright. His Majesty's Stationery Office, London. 2 shillings net. 10⅝ x 7½; 29 + 3 charts and 1 map; 1935 (paper).

Investigations undertaken to improve the South Wales oyster fishery are described. Results of the experimental relaying of Portuguese oysters in local areas are discussed and, in addition, the author has included recommendations with respect to future experimental work designed to increase the stock of local oyster beds.

Turtle Shields. *Pocket Natural History, Zoological Series No. 1.*
By Harold L. Madison. Cleveland Museum of Natural History, Cleveland, O. 7¾ x 5½; 4; 1934 (paper).

An extremely useful little leaflet that makes easy the identification of some 16 species of common turtles from external (carapace) characters. Every teaching zoologist should have this at hand.

A Child's Story of the Animal World.
By Edward G. Huey. Illustrated by H. R. Daugherty and Olive Earle. Reynal and Hitchcock, New York. $3.50. 9 x 7; 355 + 30 plates; 1936.

This is a charming zoology book for children. It is clearly and interestingly

written and the subject matter is in logical sequence. The photographs and drawings are excellent and there is a good index.

FLORIDA FISHES. *Pocket Natural History No. 5. Zoological Series No. 2.*
By Harold L. Madison. Cleveland Museum of Natural History, Cleveland, Ohio. 25 cents. 6¾ x 3¾; 32; 1936 (paper) [In envelope].

This booklet lists a number of Florida fishes and gives a brief description of the appearance and habits of each. It is well illustrated and there is an index.

BOTANY

HUMUS. *Origin, Chemical Composition, & Importance in Nature.*
By Selman A. Waksman. Williams & Wilkins Co., Baltimore. $6.50. 9 x 5⅞; xi + 494; 1936.

As an addition to the author's *Principles of Soil Microbiology* this new book on humus represents a noteworthy contribution to the field for which a need has long been felt. It is based on extensive work of the author and his coworkers as well as a thorough review of the literature. The volume contains 17 chapters which are considered in three parts, namely: a historical account of the chemical nature of humus, its formation and rôle in plant nutrition; origin in nature of humus; and the decomposition of humus, its functions and applications. The book includes also an account of methods of humus analysis. An extensive bibliography, consisting of 1311 references, adds greatly to the value of the book.

The problem of humus is not only of scientific interest but is also fundamental to aquiculture and agriculture. The large scope covered by the treatise makes it helpful to those interested in different aspects of soil study as well as to those working on problems connected with research in salt and fresh waters.

PRACTICAL PROBLEMS IN BOTANY.
By Wilfred W. Robbins and Jerome Isenbarger. John Wiley and Sons, New York. $2.00 net. 8 x 5¼; ix + 402; 1936.

Unfortunately many of these problems do not seem to us very practical so far as high-school students are concerned. Some of the problems that immature minds are asked to pass upon, are still unsolved after decades of research, and in the case of too many other questions there are no clues elsewhere in the book for a boy or girl to follow up. However, much that is good may also be said for this work. Broad principles are emphasized throughout and the authors are successful in their aim "to lay a foundation of fundamental principles which will enable pupils to develop an understanding of the significance of plant life which is such an important part of their environment." To bring out the best results from its use as a high-school text, however, the book should undeniably be in the hands of an unusually good teacher. The annotated bibliographies should be useful in selecting books for a school library. There is an index.

ELEMENTARY BACTERIOLOGY. *Third Edition, Reset.*
By Joseph E. Greaves and Ethelyn O. Greaves. W. B. Saunders Co., Philadelphia. $3.50 net. 7¾ x 5¼; 562; 1936.

The third edition of this excellent elementary textbook contains numerous additions to the subject matter treated in the previous editions (reviewed in Q. R. B., Vol. 4, p. 141; Vol. 7, p. 365). Yeasts, molds and actinomyces are discussed much more extensively and in a separate chapter. Other additions include a chapter on temporary and hereditary variations of bacteria, one on their chemical activities, and another on the lethal effect of certain chemicals on the bacteria. The popularity of this book is well deserved.

Биохимия Культурных Растений. Том I. Хлебные злаки. Н. Н. Иванов, Главный,

редактор. Государственное издательство сельскохозяйственной литературы, Москва-Ленинград. 5руб. 80 коп.; 320; 1936.

[Biochemistry of Cultivated Plants. *Vol. I. Cereals.*

Edited by N. N. Ivanoff. State Publishing House for Agricultural Literature, Moscow-Leningrad. 5.80 roubles. 7 x 10; 320; 1936 (cloth)].

The book gives a description of the chemical composition of cereals and a great attention is paid to the qualitative characteristics of the main compound substances in the plant, their accumulation and conversion in the plant organism during the vegetative period and storage in the seed. This first volume treats wheat, oats, corn, rice, millet and buckwheat. There are included an English foreword and table of contents.

Silva Fennica 34. *Viljavan Maa-alan Jakautumisesta Sekä Lehtokasvillisuudesta ja -Kasvistosta Keskisen Längelmäveden Seudulla.* [*Über die Verteilung des fruchtbaren Bodens sowie über die Hainvegetation und -Flora in den Gegenden um die Mitte des Sees Längelmävesi*].

By Olavi Cajander. Society of Forestry in Suomi, Helsinki. $9\frac{5}{8}$ x $6\frac{1}{2}$; 37; 1934 (paper). Silva Fennica 35. *Yksityismetsien Työtarjonnasta.* [*Über das Arbeitsangebot in den Privatwaldungen*].

By P. J. Pelttari. Society of Forestry in Suomi, Helsinki. $9\frac{5}{8}$ x $6\frac{1}{2}$; 17; 1935 (paper).

Silva Fennica 36. *Metsänhoitolaitoksen 75-Vuotisjuhla 19 19/IV 34.* [*75 Years' Jubilee of the Finnish Forest Service on April 19th, 1934*].

Society of Forestry in Suomi, Helsinki. $9\frac{5}{8}$ x $6\frac{1}{2}$; 78 + 1 plate; 1935 (paper).

Acta Forestalia Fennica 41. *Publications of the Society of Forestry in Suomi.* Containing following articles: *Puiden vikanisuuksista Pohjois-Suomen metsissä. Tilastollis-metsäpatologinen tutkimus,* [*Referat: Über die Schadhaftigkeiten der Bäume in den Wäldern Nord-Suomis (-Finnlands). Eine statistisch-forstpathologische Untersuchung*] by P. S. Tikka; *Koivun juuristo* [*Summary: The root system of birch, Betula verrucosa and odorato*], by Erkki Laitakari; *Kuusen juuriston ensi kehityksestä* [*Referat: Die erste Entwicklung des Wurzelwerks der Fichte*] by Martti Hertz; *Tutkimuksia metsikön ja kasvupaikan vaikutuksesta kuusen rungon kelpoisuuteen* [*Referat: Untersuchungen über die Einwirkung des Bestandes und Standortes auf die Qualität des Fichtenstammes*] by Erkki Laitakari.

Hensinki. $9\frac{1}{8}$ x $6\frac{1}{2}$; 702 + 44 plates, 1935 (paper).

MORPHOLOGY

The Cranial Muscles of Vertebrates. *By F. H. Edgeworth. University Press, Cambridge; The Macmillan Co., New York.* $30.00. $12\frac{3}{4}$ x $9\frac{1}{4}$; x + 493; 1935.

This is a superbly reproduced volume, handsomely bound, attractively printed and replete with excellent pen and ink drawings. It does credit to the printers' art. The book also does credit to its subject-matter and author since it summarizes, with admirable clarity and organization, much of the knowledge existing on the cranial musculature of vertebrates. The emphasis of the book is modestly stated by the author in the preface in which he says,

> Many investigations have been carried out during the last century and a half on the comparative anatomy and embryology of the cranial muscles of Vertebrates and of their motor nerves. I have attempted in this volume to give a summary of the knowledge that has resulted and used it to determine as far as possible the primitive cranial musculature and lower motor neurons in each of the Vertebrate phyla. The ultimate object was to ascertain what evidence this gives on the problems of their genetic relationships and so of the phylogenetic history of Man in the remote past.

For specialists in this field and for comparative anatomists generally this volume will be heartily welcomed as a detailed summary of much morphological data. The most unfortunate thing about the book is that, by virtue of its size and elaborate format, its price will be prohibitive for many students.

Einführung in die vergleichende biologische Anatomie der Wirbeltiere.

By Hans Böker. Gustav Fischer, Jena. 12 marks (paper); 13.50 marks (cloth). 10¼ x 6¾; xi + 228; 1935.

In this first volume of an introduction into comparative anatomy of the vertebrates the author has departed from the classical method of presenting comparative anatomy, the method in which emphasis is laid upon homology, and instead makes an attempt to unite the anatomical features with the life habits and environmental circumstances of the animal. In order to illustrate the dependence of form upon function, the book is divided into two main sections, the first of which deals with morphology of basic types of forms from unicellular animals down to primitive mammals; the second and by far the largest part of the book is concerned with the biological anatomy of locomotion. Seven different types of locomotion are discussed at great length in their relation to each of the classes of vertebrates. They are respectively, climbing, flying, walking and running, jumping, the upright locomotion characteristic of man, underground movements such as digging and burrowing, and swimming and diving. The author points out again and again in the book that methods of locomotion determine the habitus and appearance of an animal. The second volume will deal with the anatomy of nutrition and reproduction. An important book.

TRAITÉ D'EMBRYOLOGIE DES VERTÉBRÉS.

By A. Brachet. Second edition revised and completed by A. Dalcq and P. Gérard. Masson et Cie, Paris. 110 francs (paper); 130 francs (cloth). 9½ x 6½; viii + 690; 1935.

This is a new edition of an important embryological volume originally written by the distinguished Belgian biologist, Albert Brachet. The book has been revised by rewriting and modernizing certain parts of the text; especially the chapters dealing with gastrulation and formation of the embryo, foetal annexation and origin of the germ cells, and, by the addition of a number of new and very effective illustrations. The book is of reference calibre in that it deals minutely with many of the problems of vertebrate embryology. The text is divided into two major divisions; the first called "General Embryology" comprising a discussion of such problems as reproduction in general, structure and formation of the sex cells, fecundation, cleavage and blastulae formation and gastrulation and embryo development as illustrated by the various vertebrate groups. The second division, called "Special Embryology," is devoted to the numerous topics of organogeny. Each chapter is followed by a well-chosen and extensive bibliography.

This book, in its new edition, remains a significant and important contribution to the study of ontogeny.

PHYSIOLOGY AND PATHOLOGY

THE SPECIFICITY OF SEROLOGICAL REACTIONS.

By Karl Landsteiner. Charles C Thomas, Springfield, Ill. $4.00 postpaid. 9 x 5½; viii + 178; 1936.

The chemical aspects of immunological reactions are those in the main emphasized in this comprehensive review by a master in the field. The subject is of great importance from the point of view of general biology, especially on the theoretical side, because through immunological reactions it has been demonstrated that in living organisms chemical differences parallel differences in morphology, and with corresponding degrees of specificity. The complexity of the situation is comparable to the complexity of life itself.

The various proteins in one animal species, distinguishable by their composition and physicochemical properties, are also quite different serologically and in consequence the serum reactions reveal a two-fold specificity, that of the particular protein and, for each, that of the species. Blood serum contains at least four serologically distinct species specific proteins (globulin, fibrinogen, serum mucoid, albumin) and likewise in milk and eggs several protein antigens are demonstrable. When sera are produced with such mixtures the various antibodies corresponding to the single components can be separated without difficulty by partial precipitation. In such an experiment, after addition of a sufficient amount of horse globulin to an anti-horse, immune serum possessing precipitins for both globulin and albumin, the supernatant fluid obtained by centrifuging no longer acted on globulin, though still with undiminished intensity on albumin.

The book is extensively documented bibliographically and indexed as to subjects. It is a valuable addition to the literature of general biology as well as medicine.

DISEASE AND DESTINY.

By Ralph H. Major. D. Appleton-Century Co., New York. $3.50. 8 x 5½; xiv + 338 + 37 plates; 1936.

A book for the general reader. The author, Professor of Pathology in the University of Kansas Medical School, writes of the diseases that have had a profound effect upon world history. He shows how the destinies and thoughts of the masses have been deeply influenced by the diseases that have afflicted rulers, writers, artists and men of power. Typhus fever ended the life of Franz Schubert as well as of many lesser lights. Dürer died of malaria and St. Francis of Assisi and Molière of tuberculosis. Francis, in his youth, a gay leader of the revelers of Assisi, went through a spiritual crisis when ill of tuberculosis and subsequently became the founder of the great Order of St. Francis. It was Molière's experiences with the doctors, while ill, which supplied him with much material for his great comedies. The life of Henry the Eighth, and English history were profoundly effected by Henry's first wife (probably a syphilitic) bearing him four still-born sons and one daughter (Bloody Queen Mary). Nietsche was probably a paretic during most of the time that he was producing his writings which so deeply influenced European and American thought. Leprosy is reviewed from early times to the present. Father Damien and his work among the lepers and his subsequent death from this dread disease are given much space. Hemophilia, the curse of some of the ruling families of Europe, is discussed in the final chapter—particularly in relation to the last royal family of Russia and the devastating influence of Rasputin, whose power as a healer was sought after other sources had been exhausted in the search of a cure for the young heir to the throne.

The volume contains numerous illustrations, many of them reproductions of famous portraits and etchings, or frontispieces of books, and is indexed. Doctor Logan Clendening contributes a preface.

THE INTEGRATION OF THE ENDOCRINE SYSTEM. *Being the Fifth Horsley Memorial Lecture, Delivered at University College Hospital Medical School.*

By Sir Walter Langdon-Brown. The University Press, Cambridge; The Macmillan Co., New York. 75 cents. 7¼ x 4⅞; 54; 1935 (paper).

The purpose of this lecture was to show that both nervous and hormonal effects are important in the integration of the endocrine system. The author bases his remarks on the following three lines of advance:

1. The diencephalon (particularly the hypothalamus) has been conclusively shown to be the nervous structure concerned with the expression of the emotions.
2. The pituitary, which is so closely associated with the diencephalon, has become the leader of the endocrine orchestra.
3. It is now realized that all nervous impulses have a chemical mediator between the neuron and the tissue cell, and indeed between one neuron and another.

Growing out of this background the author visualizes the ductless glands performing their duties steadily and properly according to the biochemical demands placed on them by the body, but also, subject to much modification of their activity at certain times due to the nervous intervention of the diencephalon.

This is an interesting and scholarly lecture which synthesizes much basic material about the operation of the endocrine system as an integral, almost teleological, part of the organism.

A BASIS FOR THE THEORY OF MEDICINE.

By A. D. Speransky. Translated and Edited by C. P. Dutt with the Collaboration of A. A. Subkov. International Publishers, New York. $4.00. 9 x 6; 452; no date.

This is a remarkable book, impossible to review adequately in a brief paragraph because it is made up of a mass of experi-

mental details and theoretical interpretations of them, without any clear cut general organization of the material into a unified whole. It represents well the best and the worst of Soviet science today; extraordinary brilliance and originality of experimentation and detailed thinking, on the one hand; painfully little and inadequate coherent organization of ideas, synthesis, and generalization.

One aspect of Speransky's position can be put in this way. The current view of the mechanism of infectious disease is that the disease arises from the victory of an invading microbe over the defensive resources of the organism—a view which holds also that the whole course of the disease is determined by the struggle between the micro-organism and its host. Speransky, on the contrary, argues that not only the course but the cause of the disease changes with every stage. It is a process depending on the interaction of many parts. It should be pictured as a chain of reactions, proceeding essentially in the nervous system, with every link determined by its predecessor.

We strongly recommend the reading of this book to medical men, physiologists, and general biologists.

La Renaissance de la Médecine Humorale.

By Auguste Lumière. Léon Sézanne, Lyon. 20 francs. $8\frac{1}{2}$ x $5\frac{1}{4}$; xi + 204; 1935.

This is a diffuse and rather vague exposition of the author's theory regarding the humoral changes associated with disease. It is contended that, since a number of substances which enter into the composition of body cells and tissues are in the colloidal state and since metabolic changes and toxins will cause flocculation of the colloids, the precipitates will irritate the sympathetic nerve endings and give rise to such conditions as asthma, anaphylactic shock, etc., and the symptoms which accompany fevers, vomiting, headaches and the like. Therefore, he concludes, whenever humoral changes accompany disease, the patient should be treated with substances that either will assure greater stability of the colloids or will decrease the irritative power of the precipitates. He has found that magnesium hyposulphate among other things has these properties, and in the reports of successfully treated asthma cases the efficacy of this compound as a therapeutic agent is extolled.

Much to the author's manifest chagrin this theory, which he has advanced since 1921, has attracted little or no attention in medical circles. The reasons for such disregard are not very difficult to understand. The introduction to this volume contains an excellent summary of the history of humoral theories in medicine.

Le Testicule. *Organe Élaborateur de l'Hormone Sexuelle Mâle. Actualités Scientifiques et Industrielles 259. Exposés de Biologie. La Cellule Germinale dans l'Ontogenèse et l'Évolution, III.*

By Jacques Benoit. Hermann et Cie, Paris. 15 francs. 10 x $6\frac{1}{2}$; 64; 1935 (paper).

L'Ovaire. *Organe Élaborateur des Hormones Sexuelles Femelles. Les Hormone-Sexuelles chez les Intersexués. Actualités Scientifiques et Industrielles, 260. Exposés de Biologie. La Cellule Germinale dans l'Ontogenèse et l'Évolution, IV.*

By Jacques Benoit. Hermann et Cie, Paris. 15 francs. 10 x $6\frac{1}{2}$; 68; 1935 (paper).

These two brochures contain a very good review of the literature, together with a presentation of some work of the author, on the development of the ovary and testes. There is nothing essentially new. From morphological and histophysiological studies on birds, fishes, amphibians, reptiles and mammals the author confirms the notion held by some other workers in the field that the embryonic gonad, male or female, is originally bi-sexual, and that whether it develops into ovary or testis is determined by the cortex-medulla complex. It is suggested that even among normals an activity of a hetero-sexual hormone can be realized up to a certain point and only slightly impair a one hundred per cent sexuality.

A Bibliography of Two Oxford Physiologists, Richard Lower 1631–1691, John Mayow, 1643–1679. *Oxford Bibliographic Society Proceedings and Papers, Vol. IV, Part I.i, 1934.*

By John F. Fulton. Oxford University Press, Oxford. 10 shillings. 10¼ x 7½; 62 + 6 plates; 1935 (paper).

This bibliography is of value because it represents the works of two scientists who were among the first to enter the field of experimental physiology at Oxford University. The author, who has already prepared a bibliography of Robert Boyle and hopes in the future to compile other bibliographies of men prominent in Oxford science during the Restoration, gives all the known editions of these men's writings together with notes, explanations and discussions. Dr. K. J. Franklin contributes an introduction to Lower. Naturally, it is Lower's bibliography that is now of greater importance and interest, but during their time, both Lower and Mayow were widely read, as this list of their works with frequent editions testifies. The author includes brief biographies of both, and sections regarding those writings in which their work was discussed and criticized. Reproductions of a number of facsimiles of title pages add considerable interest to the text. Technically the work maintains the high standards of the author's earlier excursions into the field of bibliography.

L'Ivresse (*Physiologie de l'aliment excitant*). *Actualités Scientifiques et Industrielles*, 265.

By J. A. de Loureiro. Hermann et Cie, Paris. 10 francs. 10 x 6½; 38; 1935 (paper).

Physicians and physiologists, whether they believe that alcohol and other stimulants are harmful to man or whether they believe them beneficial, apparently overlook the most important point, which is that man has recourse to stimulants because he desires them. This is the substance of the author's brief but interesting discussion on inebriety. While it is principally of alcoholic inebriety of which he speaks, the term used is intended to cover the state of excitation due to sexual, religious, artistic and other stimuli. In his opinion, the desire for these as well as for alcoholic stimulants are typically human and should be considered as such by the physiologist.

The Avian Visual System. *I. Cerebral Function of the Domestic Fowl in Pattern Vision. Comparative Psychology Monographs, Vol. 12, No. 3, Serial No. 58.*

By John D. Layman. Johns Hopkins Press, Baltimore. 75 cents. 10 x 7; 36; 1936 (paper).

In the experiments reported here, the author destroyed by electric cautery varying amounts of the cerebral cortex and assayed the effect of this operation on the ability of the domestic fowl to discriminate visual patterns. It was found that the cortex was not essential to vision; a fact in contrast to the results obtained by investigators working with mammalian forms. However, the ability to discriminate in visual learning did vary directly with the amount of cortex destroyed. Birds with large cortical lesions learned more slowly and with less success than did those with small lesions.

Lésions du Pancréas et Troubles Fonctionnels Pancréatiques. *Diagnostic en Clinique par l'Épreuve a la Sécrétine Purifiée.*

By Marc Bolgert. Masson et Cie, Paris. 45 francs. 9¾ x 6½; viii + 255; 1935 (paper).

A resumé, with an extensive list of case histories and observations, of the author's work on pancreatic dysfunction as ascertained by the purified secretin test. The first part of the book is confined to technique and interpretation of the test; the second and third parts, to results as obtained in diseases of the pancreas, the liver and gall bladder, digestive tract, colitis, the anemia of Biermer and other ailments. The author concludes that pancreatic disorders are more common in diseases other than those primarily of this organ, than is ordinarily supposed. Fourteen pages of bibliography are included.

DIE HERSTELLUNG UND PRÜFUNG HOMÖOPATHISCHER ARZNEIMITTEL. *Eine Anleitung für das Apothekenlaboratorium.*

By Konrad Schulze. Theodor Steinkopff, Dresden. 4.50 marks. $8\frac{3}{4}$ x $5\frac{3}{4}$; viii + 92; 1936 (paper).

This is a useful guide for the pharmacists who are called upon to prescribe and concoct homeopathic remedies. It is based more or less upon an earlier work by Hahnemann, the *Urgrossvater* of homeopathy; this work being now in its sixth edition. All the latest pill mixing, pulverizing, and drying machines are described. The brochure is probably more valuable for German apothecaries, who have often considerable medical knowledge, than for American pharmacists.

GLANDULAR PHYSIOLOGY AND THERAPY. *A Symposium.*

Prepared under the Auspices of the Council on Pharmacy and Chemistry of the American Medical Association. American Medical Assoc., Chicago. $2.50. $8\frac{3}{4}$ x $5\frac{1}{2}$; vi + 528; 1935.

In this series of articles (32) written by specialists, the clinician has at hand authoritative information concerning what is established and what is still theoretical in this important field. The articles originally appeared in the *Journal of the American Medical Association* but have been revised where necessary before publication in book form. Each section is thoroughly documented. The detailed index will be found highly useful. For the general biologist the volume furnishes a valuable summary of endocrinology to date.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 449. Methoden der Muskel- und Nervenphysiologie.* Containing following articles: *Myothermische Schnellregistrierung mittels des Elektronenröhren-Mikrovoltmeters,* by Edgar Wöhlisch; *Röntgenuntersuchung der Knochen und Gelenke,* by Rudolf Grashey; *Methoden zur Untersuchung der glatten Muskulatur der Lunge,* by Manfred Kiese; *Eine Kathodenstrahloszillographeneinrichtung für physiologische Zwecke,* by Leon Asher; *Tätigkeitssubstanzen der quergestreiften Muskulatur,* by Gustav Embden and Gerhard Schmidt; *Mikrobestimmungen von Purinsubstanzen in Geweben,* by Gerhard Schmidt.

Urban und Schwarzenberg, Berlin. 14 marks. 10 x 7; 224; 1936 (paper).

The papers in this volume describe new methods of study of nerve muscle physiology. They are mostly concerned with the use of electricity and cathode rays in experimentation. One paper describes a method of registering heat production from muscle by means of a newly invented instrument—*Electronenröhren-Mikrovoltmeter.* This instrument is considerably more sensitive to thermal changes than others commonly used.

BIOCHEMISTRY

THE CHEMISTRY OF NATURAL PRODUCTS RELATED TO PHENANTHRENE.

By L. F. Fieser. Reinhold Publishing Co., New York. $6.50. 9 x 6; xii + 358; 1936.

This is a highly technical discussion and review of the present state of knowledge about the chemistry of a considerable number of substances of great interest to biologists just now. Unless they are also trained organic chemists, however, much of the book will be right over their heads —modern coal tar chemistry is distinctly not a subject that can be lightly taken in one's stride. Phenanthrene is a hydrocarbon isomeric with anthracene. Natural products that are derivatives of, or closely related to phenanthrene, include such things as the cancer producing hydrocarbons, the alkaloids of the morphine and aporphine groups, the sterols and bile acids, the sex hormones, the cardiac glycosides and toad poisons, and the saponines including those of the digitalis group. So it is plain that phenanthrene is a juice that the biologist has sooner or later got to know about. Dr. Fieser points the way with great skill and learning; no blame can attach to him if the road itself seems to the biologist to be a tough and rocky one.

ÜBER KATALYTISCHE VERURSACHUNG IM BIOLOGISCHEN GESCHEHEN.

By Alwin Mittasch. Julius Springer, Belin. 5.70 marks. 8½ x 5¾; x + 126; 1935 (paper).

This book, written by a chemist, reviews and summarizes what is known, or thought, up to the present time concerning the properties and teleology of the catalytic factors in ferments, enzymes, hormones, vitamins, growth stimulation substances, genes, etc.; their interrelationship and effect on the organism as a whole. The author concludes that:

> The totality of the biocatalyzers of an organism appears to be an ordered system of lower teleocausal factors, which are under the authority of the law of life, that is, at the service of the higher aim of the organism (with its higher powers of "*Biofeld*") and which are necessary for the chemistry of life throughout all its stages. The biocatalyzer directs and is directed.

PRÉCIS DE CHIMIE. *A l'Usage des Candidats au Certificat d'Études Physiques, Chimiques et Biologiques et a la Licence ès Sciences.*

By A. Tian and J. Roche. Masson et Cie, Paris. 80 francs. 7⅝ x 5¼; viii + 970; 1935.

A chemistry text intended for students of medicine and biology and written with the express purpose of meeting the new requirements for a doctor's certificate. The book is divided into five parts. Part I is a brief survey of inorganic chemistry and physical chemistry dealing mostly with such general principles as valence, states of equilibrium, electrolysis, etc. Part II deals with hydrogen in great detail. Part III with metals and the various derivative salts, with a concluding section on organic chemistry. Part IV deals with the fatty acid series, and Part V with cyclic structures such as the benzene ring, etc.

REPORTS OF THE BIOCHEMICAL RESEARCH FOUNDATION OF THE FRANKLIN INSTITUTE (*Formerly the Cancer Research Laboratories*), Vol. III, 1934–1935.

Franklin Institute, Philadelphia. 9¾ x 6¾; collection of reprints.

A bound collection of reprints by various members of the staff of the Foundation. Some 27 of them deal with biochemical subjects related generally to the metabolism of tumors, while 6 are statistical papers on cancer by Dr. F. L. Hoffman.

KOLLOID-FIBEL FÜR MEDIZINER.

By Raphael E. Liesegang. Theodor Steinkopff, Dresden and Leipzig. 1 mark. 8¾ x 5½; 34; 1936 (paper).

A concise, authoritative summary of the chemical, physical and anatomical properties of the colloids, written primarily for medical men. An index of colloid-chemical terms is appended.

SEX

LA DÉTERMINATION DU SEXE ET L'HÉRÉDITÉ. *Actualités Scientifiques et Industrielles 258. Exposés de Biologie. La Cellule Germinale dans l'Ontogenèse et l'Évolution. II.*

By Émile Guyénot. Hermann et Cie, Paris. 20 francs. 10 x 6½; 79; 1935 (paper).

The distinguished pioneer in *Drosophila* genetics who contributes this brochure to the lively *Actualités* series, gives an interesting, stimulating and critical appraisal of the present theoretical position regarding sex determination. Starting from the point that sex is determined at fertilization, he is of that opinion that as a general rule all individuals inherit the opposed factors of masculinity and femininity which have the tendency to orient the general processes of metabolism in different directions. Sexual differentiation is to be regarded as the resultant of the equilibrium established between these two antagonistic tendencies. The experimental results on environmentally altering the genotypic sex ratio in batrachians are accepted, and interpreted as indicating that what we call factors of sexuality are primarily factors of nutrition—regulators of metabolism—that can be operated in more than one way. Great importance

is attached to the results of Dobzhansky and Schultz showing the multiplicity of feminising factors in the X chromosome of *Drosophila*, because they lend support to the metabolic viewpoint of the author. The problem of intersexuality is discussed. As a document of the "day and fray" this pamphlet will interest the geneticists.

PSYCHOLOGY OF SEX. *A Manual for Students. By Havelock Ellis. Emerson Books, New York.* $3.00. 8½ x 5½; xii + 377; 1935.

The author's reason for writing this book can best be stated in his own words,

> . . . there is need for a small book to serve as a concise introduction to Sex Psychology. Ordinary medical practitioners and students, it is said, are far too overburdened already to be able to master extensive treatises on an additional subject which is not obligatory. The subject of sex in its psychic and social bearings is so central, and of an importance now so widely recognized, if not indeed exaggerated, among the general public, that the medical man of today cannot fail to have it brought before him. He cannot, like his predecessors, conventionally ignore its existence, or feel that its recognition would be resented as impertinent or indecorous. Moreover, a knowledge confined to general anatomy, physiology, and pathology is now altogether inadequate.

The book deals with such topics as the biology of sex, the sexual impulse, homosexuality, marriage, the technique of love, etc., and is beautifully written, as is to be expected from the great master. A bibliography follows each chapter and a short glossary and index follow the text.

ENCYCLOPAEDIA SEXUALIS. *A Comprehensive Encyclopaedia-Dictionary of the Sexual Sciences. Edited by Victor Robinson. Dingwall-Rock, New York.* $7.50. 9⅜ x 6¼; xx + 819; 1936.

This is a book of 819 pages covering a variety of medical-biological-sociological-legal topics loosely bound together by the ambiguous term "sex." [Reginald, the Office Boy, says it doesn't seem ambiguous to him, especially in the spring]. The material is treated in encyclopaedic fashion with the various topics discussed in alphabetical order. For each entry there is presented an etymological interpretation of the term in question; a historical sketch of the subject matter where pertinent; an explanation of the subject in the light of contemporary knowledge, and a list of references.

With the individual articles we have no quarrel: most of them, by and large, seem to be creditably written and quite authoritative. Indeed the book prospers by having had the services of some distinguished specialists—Briffault, Lillie, Morgan and others. Our serious quarrel with the book is concerned with the actual need for such a volume at all. It is certainly at best a very loosely integrated production and it seems doubtful that it will fill a real place in the libraries of any but the sexually curious.

PHYSIOLOGY OF LOVE. *By Paolo Mantegazza. Translated from the Italian by Herbert Alexander. Eugenics Publishing Co., New York.* $3.00. 9⅜ x 6¼; xviii + 237; 1936.

When the first edition of this book appeared in Italy some sixty years ago, the moralists reacted to it in the same indignant fashion as those of the present day have condemned books on contraception, free love, etc. A generation later this book was considered to have some instructive value. Now it is entirely outmoded. To the reader of modern sex books which reflect a more or less morbid outlook, Mantegazza will appear naïve. Yet, if the translater had avoided such a faithful rendition of the author's redundent and florid style, common in the Italian prose of the period, this book would serve a good purpose. The fact is that Mantegazza was a keen student of human biology, and in this volume he described the range of variation of that complex of psychic and physical manifestation called love, which he saw as a purely biologic phenomenon that transcends morality. A better and modernized translation should make this book popular for the layman who is not interested in pathologic sex problems.

TIME OF OVULATION IN WOMEN. *A Study on the Fertile Period in the Menstrual Cycle.* *By Carl G. Hartman. The Williams and Wilkins Co., Baltimore.* $3.00. 7¾ x 5¼; x + 226; 1936.

The chief purpose of this volume is "to furnish the busy practitioner, . . . , a concise yet comprehensive survey of the essential facts concerning the period of ovulation in women." It is an authoritative treatise. While there still remains much research to be done on this subject the author states that "the opponents of the Safe Period are more and more placed on the defensive as new facts accumulate." The first nine chapters of the book contain brief summaries of the physiological facts concerning germ cells, fertilization, sex cycles, etc. The latter and larger part of the volume deals with the time of ovulation. The work includes figures, tables and graphs, an appendix of 54 notes on the chapter which deals with the age of human embryos, a lengthy bibliography with annotations, and an index.

PROSTITUTION IN THE MODERN WORLD. *A Survey and a Challenge.* *By Gladys M. Hall. Emerson Books, New York.* $2.00. 8⅜ x 5½; 200; 1936.

This is a superficial summary of what little actual information there is regarding the extent and practice of prostitution. The few facts which the author does not quote from well-known publications are derived from sources of dubious value such as "a Harley Street specialist," "a Canadian ex-army captain." Briefly told, the author believes that the "professional" prostitute is now being superseded by the "amateur," and finds the cause of this occupational shift in the "new morality." It is well to remember that similar statements were made at various times in ancient Greece and Rome, during the Renaissance, and at various later periods, but still "professional" and "amateur" prostitution and the institution of monogamous marriage have all along persisted side by side.

THE SINGLE, THE ENGAGED AND THE MARRIED. *By Maurice Chideckel. Eugenics Publishing Co., New York.* $2.50. 8 x 5⅜; xxxiii + 270; 1936.

This is a discussion, couched in a somewhat poetic vein, of the many physiological and psychological problems of sex as viewed through the eyes of the consulting clinician. The book attempts to give information about both normal and abnormal sexual relationships and to suggest practices and procedures calculated to guide the "single, the engaged and the married" into healthful and sane sex habits. It does not differ greatly from the usual run-of-mine sex books and can be read without harm, and with possible enlightenment, by the general public.

BIOMETRY

PROBABILITY AND RANDOM ERRORS. *By W. N. Bond. Longmans, Green and Co., New York.* $3.75. 8⅝ x 5⅜; viii + 141; 1935.

In this book, primarily addressed to students of physics and chemistry, the author presents the elements of the theory of probability. The order follows that of the standard elementary textbooks, but a judicious selection of examples permits the student to arrive at a real understanding of the field of application of the probability theorems. The subject matter includes sections on permutations and combinations, calculation of the fundamental statistical constants, distribution of errors, probable errors of diverse functions, correlation, curve fitting and periodogram analysis. The numerous and interesting examples make this a useful book especially for the biostatistician who will get some new ideas from them. It is well to note, however, that the method of demonstrating the derivations of some of the formulae could have been simpler and more straightforward. In common with other textbooks on the subject, the author fails to emphasize at all times the conditions which are necessary in order to obtain significant results by the use of the formulae.

DIE VARIABILITÄT DER ORGANISMEN *und ihre Normgrenzen. Zugleich ein kurzer Leitfaden der Variationsstatistik.*

By Hans Günther. Georg Thieme, Leipzig. 7 marks. $9\frac{3}{4}$ x $6\frac{3}{4}$; 132; 1935 (paper).

This monograph discusses statistical methods for measuring variation in human physical, physiologic and mental characteristics. The author introduces the subject with a brief exposition of the principles of genetics, and of genotypic and phenotypic variability. This is followed by a detailed description of the methods of calculating the statistical constants in common use. A number of chapters are dedicated to a summary of the several concepts regarding the limits of "normality." While the subject has been amply treated by numerous biostatisticians, the author's clear presentation will certainly be found useful. The bibliography is adequate.

AN OUTLINE OF PROBABILITY AND ITS USES.

By Maurice C. Holmes. Edwards Bros., Ann Arbor, Michigan. $1.50. $8\frac{1}{4}$ x $5\frac{1}{4}$; viii + 119; 1936 (paper).

This is a compendium of the elementary formulae of the theory of probability, their derivations and uses. In a clear and brief manner the author discusses combinations and permutations, Bernouilli and Poisson distributions, the normal probability curve, Bayes' theorem, the chi-square test and correlation coefficients. The examples and problems will be found useful by the student, and special mention should be made of the well chosen list of reference books.

WIDTH-WEIGHT TABLES. *For Boys and Girls from 1 to 16 Years. For Men and Women from 17 to 24 Years.*

By Helen B. Pryor. Stanford University Press, Stanford University, Calif. Single copy, 60 cents; 2–4 copies, 50 cents each; 5–9 copies, 40 cents each; 10 or more copies, 35 cents each. $8\frac{1}{2}$ x $5\frac{1}{2}$; 15; 1936 (paper).

These tables are constructed so as to offer a range of seven normal weights for each height and age depending upon the width of the iliac crest. The recognition of varying bodily habitus types is important and the figures appear to be based on a sufficiently large number of cases to be dependable.

PSYCHOLOGY AND BEHAVIOR

AN ENQUIRY INTO PROGNOSIS IN THE NEUROSES.

By T. A. Ross. The University Press, Cambridge; The Macmillan Co., New York. $3.00. $8\frac{1}{2}$ x $5\frac{1}{2}$; ix + 194; 1936.

In the preface, the author justly observes that "knowledge in prognosis has lagged considerably behind other medical knowledge" and that only by statistical surveys can one hope to arrive at an adequate evaluation of therapeutic measures. In this book he discusses the results of the treatment of some 1200 patients of the Cassell Hospital for Functional Disorders, Kent, England. The report is based on all the information obtained from the patients in response to letters of inquiry sent by the author at regular intervals after the patient's discharge from the hospital. Such information is, of course, not always reliable but the author appears to be well aware of this and proceeds with characteristic caution and objectivity in drawing his conclusions. The data, which consist of cases admitted in the hospital from 1921 to 1933, are reported in full and include information regarding sex, age, duration of symptoms, duration of hospitalization, symptoms on admission and state of patient annually since discharge. A number of cases are discussed in detail and used as illustrative examples. The author arrives at conclusions somewhat at variance with those of the Freudian School. He believes that in a number of cases permanent benefit may be obtained with short courses of treatment, by substituting teaching for analysis and without the necessity of exploring the infantile unconscious.

The prognosis is remarkably good for patients with anorexia nervosa but improvement is seldom seen in those with

obsessional compulsive neurosis. The results in traumatic neurosis, he finds, are dependent generally on the nature of financial compensation. For a patient with frank neurosis, the risk of committing suicide or becoming insane is rather small. These and other facts lead the author to affirm that neurosis and psychosis are not different degrees of the same thing.

While from the statistical standpoint the elaboration of the data leaves much to be desired, yet the recognition that this is the method of approach for a determination of prognosis and the author's impartial and detailed discussion of the results, make this book a useful contribution to psychiatry and medicine.

ESSENTIAL TRAITS OF MENTAL LIFE. *The Purposes and Principles Underlying the Selection and Measurement of Independent Mental Factors, Together with Computational Tables.* *By Truman L. Kelley. Harvard University Press, Cambridge.* $2.75. $8\frac{1}{2}$ x $5\frac{5}{8}$; 145; 1935.

A hand book for students engaged in the analytical study of personality. It is volume 26 in the Harvard Studies in Education. The chapter headings are as follows: A new method of analysis of variables into independent components, Various approaches to the analysis of mental traits, Comparison of components determined by the principal axes method and by the center of gravity method, Social impositions upon the problem of the analysis of mentality, Factors suggested by sundry judgments, and Worksheet and table facilitating the rotation of axes. In this study, a continuation of the author's investigations in the number, nature and relationship of mental traits, is developed a concept of *trait*, "a joint result of original tendencies and surrounding social impositions." The volume contains numerous formulae, 22 tables, charts (trait ratings by occupational groups, sample ratings for abridged population to show procedure, and revised sample ratings for first trait). There are also given select bibliographies on (a) Recent literature dealing with the two factor theory and especially with the question of the uniqueness of "g"; (b) Recent discussions of factor analysis techniques; (c) Recent discussions of mental organization; (d) Recent experimental studies using factor analysis techniques. The volume is indexed.

A REPORT ON TWO EXPERIMENTAL FIRE-WALKS. *Bulletin II.* *By Harry Price. University of London Council for Psychical Investigation, London.* 5 shillings net (Foreign, $1.25). $9\frac{1}{4}$ x 6; 15 + 20 plates; 1936 (paper).

Practically everyone, at one time or another, has heard stories of native peoples walking, during ceremonial rites, over stones heated to uncomfortable temperatures and apparently suffering no ill effects therefrom. These stories, however, have frequently caused the judicious to express some disbelief as to their authority and wish that an honest, realistic test of them would be forthcoming. It appears that such a report is available in the present paper in which the author describes his observations on two experimental fire-walks conducted by an East Indian in the quiet surroundings of an English countryside. As a result of his researches the author comes to the conclusion, "... that it is possible, for a slightly-built man with chemically unprepared feet, to take four rapid steps on charcoal at 430° Centigrade, without injury to his feet, the average time of contact for each step being approximately half a second. It is hardly necessary to point out that, in rapid walking, the whole of the foot is not put into contact with, or withdrawn from, the ground at one instant, so that *no one portion* of the skin was in contact with the hot embers for as long as half a second. This may therefore be regarded as an upper limit to the time of continuous contact."

THE MIND OF THE DOG. *By F. J. J. Buytendijk. Translated by Lilian A. Clare. Houghton Mifflin Co.,*

Boston. $2.50. 8 x 5¼; 213 + 20 plates; 1936.

This analytical study of the dog's behavior, by a Dutch physiologist in the University of Groningen, is of importance to the behaviorist. It will also interest all dog lovers, although they will sometimes disagree with his conclusions. The author was chiefly occupied in studying the functioning of the organs of sense, impulses, formation of habits and insight in unfamiliar circumstances of life. He did not limit his observations to experimental investigations but closely observed the animals in their natural surroundings. His own tracking experiments agree with those of other workers, namely—that the dog is by no means infallible in following human trails. He is not convinced that a dog really understands our words for, "in my opinion there is scarcely one experiment that is perfectly safe for ascertaining the understanding of words." In habit forming "we have come to realize more and more that in all learning *insight* is also operating and that there is really no action without insight." Numerous experiments of his own and others are cited to make clear his position on this point. A section is devoted to Pavlov's experiments. The volume is well illustrated but is without an index.

ADULT INTELLIGENCE. *A Psychological Study of Test Performances.*

By Theodore Weisenburg, Anne Roe and Katharine E. McBride. The Commonwealth Fund, New York. $1.40. 9¼ x 6⅛; xiii + 155 + folding table; 1936.

This is a report of an extensive and thorough study by intelligence testing methods on groups of adult hospital patients, normal as to mentality in the sense of having no discernible mental disease. Among the many interesting details brought out, the authors find that by far the greatest extent of mental development occurs before the twenties, while from that decade through the fifties there is little change, either way by further gains or in the direction of loss. The amount of formal schooling was found to be probably not as important a factor as it is usually supposed to be. The intelligent man with poor schooling compensates in adult life for his lack. The dullard with a lot of schooling has either forgotten most of it by adult life, or it never really "took" at any time. Sex differences were found to be negligible.

There is a substantial bibliography and an index.

THE PROBABILITY OF COMMITMENT FOR A MENTAL DISORDER OF ANY KIND BASED ON THE INDIVIDUAL'S FAMILY HISTORY. *Monograph Series Number X.*

By Serge Androp. Eugenics Research Association, Cold Spring Harbor, Long Island, N. Y. 50 cents. 9 x 6; vi + 79; 1935 (paper).

The author presents and summarizes the pedigree charts of 54 families, each of which is characterized by the fact that at least one member of the family, being either feebleminded, epileptic or insane, has been committed to some institution. The results show that the percentage of commitments is a minimum for the offspring of parents with a negative family history of mental disorders; it is a maximum for those individuals both of whose parents belong to families with a high incidence of these mental disorders.

Before any judgment can be passed regarding the validity and significance of such results, it is necessary that the author revise his method of analysis. It is remarkable that this, a prize winning monograph of the Eugenics Research Association, should have been permitted to appear in print when it contains a major logical error: the assumption that the "probability of commitment for a mental disorder" could be estimated from such selected population.

GRUNDLAGEN DER RASSENPSYCHOLOGIE.

By Egon F. von Eickstedt. Ferdinand Enke, Stuttgart. 5.40 marks (paper); 6.80 marks (cloth); 25 percent reduction outside of Germany. 9 x 5¾; 164; 1936.

The author believes that a comprehensive

and workable system of race psychology can only be obtained from a thorough study of a wide range of branches of human biology. In this book he reviews critically the more important literature on racial and individual psychology, anthropology, ethnology, human constitution, etc., in an effort to work out some system of methodology which will enable one to differentiate traits which can fundamentally be attributed to race, and race only, from those due rather to environment or other factors. In the current so-called intelligence tests used in an attempt to find mental differences among the races he finds much to be desired. Students of human biology should find this thought-provoking book of interest. It is well documented and there is an index of authors.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

A World of Chance *or Whence, Whither, and Why?*

By Edward G. Spaulding. The Macmillan Co., New York. $3.00. 8 x 5½; xxxiii + 293; 1936.

This is a forthright treatise by the distinguished McCosh Professor of Philosophy at Princeton. It has been evident lately that a good many of the Elder Statesmen of biology, whose periodic ejaculates of accumulated and concentrated wisdom in committee rooms keep our science in safe channels, were beginning to be vaguely disturbed by all this loose talk of the physicists about the "principle (God save us!) of indeterminism." Nicely brought up intellectually, they dislike such slightly blasphemous even if playful monkey business with the Sacred Things, like cause and effect. Youth tends to ebullience, of course, but these are serious times frought with such dangers that the boat had better not be rocked. Indeed (just between ourselves and don't quote me), just as Mr. Roosevelt and Mr. Farley are taking steps to implement the obvious deduction that this would be a better world if it contained no Republicans, perhaps a hint in the right place might lead to a safer and saner allotment of funds to right-minded physicists, and then all this nonsense would be soon stopped.

It is too bad, but *A World of Chance* is destined to give the old dears a dreadful jolt. For Dr. Spaulding not merely grasps the sprightly bullock of indeterminism firmly by the horns, but hangs a *lei* of high-toned mathematical logic around its neck, suspends a halo above its head, and by the clever exhibition of various sorts of hormone therapy does his level best to transform this mischievous he-devil into a Sacred Cow of Scientific Respectability. To the queries of the subtitle Whence, Whither, and Why? the answers, in clarion tones are: From no Source, To no End, and For no Reason. So far from indeterminism perhaps occasionally playing a small trick on earnest thinkers, it is the whole works.

Far be it from us to say whether the book establishes its thesis. So great is the influence of our lightest word that to do so might deter some of our customers from reading it, and thus deprive them of the pleasure thereby to be gained. It must suffice to say that the argument is shrewd and clever. The terminology of mathematical logistic in which a good part of it is couched is a bit forbidding, and undoubtedly—and also unfortunately—takes the book right out of the realm of easy or rapid reading. But it is a book that had best not be neglected.

Why Keep Them Alive?

By Paul de Kruif, in collaboration with Rhea de Kruif. Harcourt, Brace and Co., New York. $3.00. 8½ x 5⅞; 293; 1936.

In a sentence, this, the latest book by Paul de Kruif, could be characterized as follows: We know a lot about the technique of reducing child mortality, morbidity and general suffering—isn't it just terrible that all that is known is not universally practised? In other words, why is any child ever allowed to suffer when medical science is so able to help them? The answer suggested, mainly but not entirely by indirection, is that when the present economic and social system shall have been overset and all the fit and provident folk

now able to take care of themselves in an ungentle world have been forcibly put under the domination of the less fit, who are so to be pitied now because they do not get all of the best the world has to offer, then all will be well or at the very least a great deal better. Such diverse subject matter as the treatment of burns, hunger and the problem of child nutrition, tuberculosis, *and* the Dionne quintuplets is utilized to pile horror on horror.

The book is in essence a piece of exaggerated emotional propaganda for the extension of public health services. The further development and extension of public health is wholly to be desired, and is in fact occurring all the time by normal processes of social evolution. Past experience has demonstrated however that its orderly progress has not been helped, but rather hampered, by emotional overstatements of the case before the court of Common Sense, J., sitting with Humanity, J. and Decency, J.